Helsinki University of Technology

Systems Analysis Laboratory Research Reports A102, December 2008

THE LIGNUM FUNCTIONAL-STRUCTURAL TREE MODEL

Jari Perttunen

TEKNILLINEN KORKEAKOULU
TEKNISKA HÖGSKOLAN
HELSINKI UNIVERSITY OF TECHNOLOGY
TECHNISCHE UNIVERSITÄT HELSINKI
UNIVERSITE DE TECHNOLOGIE D'HELSINKI

Helsinki University of Technology

Systems Analysis Laboratory Research Reports A102, December 2008

THE LIGNUM FUNCTIONAL-STRUCTURAL TREE MODEL

Jari Perttunen

Dissertation for the degree of Doctor of Philosophy to be presented with due permission of the Faculty of Information and Natural Sciences for public examination and debate in Auditorium E at Helsinki University of Technology (Espoo, Finland) on the 13th of February, 2009, at 12 noon.

Helsinki University of Technology
Department of Engineering Physics and Mathematics
Systems Analysis Laboratory

Distribution:

Systems Analysis Laboratory

Helsinki University of Technology

P.O. Box 1100

FIN-02015 HUT, FINLAND

Tel. +358-9-451 3056

Fax +358-9-451 3096

systems.analysis@hut.fi

This report is downloadable at

www.sal.hut.fi/Publications/r-index.html

ISBN 978-951-22-9709-2

ISBN (pdf) 978-951-22-9710-8

ISSN 0782-2030

Espoo 2008

Title: The LIGNUM functional-structural tree model

Author: Jari Perttunen

Finnish Forest Research Institute
Jokiniemenkuja 1
PL 18, FIN-01301 Vantaa, Finland
jari.perttunen@metla.fi

Date: December 2008

Abstract: The aim of this thesis was to construct a single tree model that builds a bridge between traditional process based tree models and detailed, three-dimensional architectural tree models. The result of the thesis, the functional-structural tree model LIGNUM, integrates both the functional and the structural aspects of woody arborescent plants in a single generic modelling framework.

The thesis consists of five articles and the summary part. The first article presents the model structure of LIGNUM based on simple recurring botanical units, their metabolic processes and the allocation of photosynthates on the basis of the carbon balance resolved according to the specific growth potential in different parts of the tree crown. The model is applied to young Scots pine (*Pinus sylvestris* L.). The second article studies alternative formulations of sapwood senescence in Scots pine. The third article presents an improvement in assessing solar radiation absorption on the basis of the mutual shading of tree segments. The fourth article adapts the LIGNUM model to deciduous species with sugar maple (*Acer saccharum* Marsh) as an example. The fifth article introduces Lindenmayer systems for defining the architectural development of the tree crown.

The central problem in process-based tree models has been resource capture and allocation in a dynamically growing tree. The main contribution of this thesis is to present a solution to how photosynthates can be allocated among possibly thousands of botanical units in a tree. The LIGNUM model can simulate the three-dimensional architectural development of a tree crown, keep track of each elementary functional unit, define their local capacity to produce and use resources, and determine the interactions with each other and the external environment.

Keywords: Functional-structural model, tree physiology and architecture, Lindenmayer systems, growth allocation.

Otsikko: Puun rakenteen ja toiminnan malli LIGNUM

Tekijä: Jari Perttunen

Metsäntutkimuslaitos
Jokiniemenkuja 1
PL 18, FIN-01301 Vantaa
jari.perttunen@metla.fi

Päiväys: Joulukuu 2008

Tiivistelmä: Tämän väitöskirjan tarkoituksena on ollut tehdä puun kasvumalli, joka yhdistää perinteiset puun elinotoimintojen kuvaamiseen perustuvat prosessimallit ja puun arkkiehtuurimallit, jotka mallintavat latvuksen kolmiulotteisen rakenteen. Tämän työn tulos, puun rakenteen ja toiminnan malli LIGNUM, ottaa huomioon puun fysiologisen toiminnan ja sen rakenteen väliset dynaamiset vuorovaikutukset.

Väitöskirja kostuu viidestä osajulkaisusta ja yhteenveto-osasta. Ensimmäinen osajulkaisu esittää LIGNUM -mallin rakenteen yksinkertaisten rakenneosien joukkona, näiden rakenneosien fysiologiset prosessit ja yhteyttämistuotteiden allokaation perustuen hiilitaseeseen, joka ratkaistaan puun latvuksen eri osissa olevan erilaisen kasvupotentiaalin perusteella. Mallia sovelletaan nuorelle männylle (*Pinus sylvestris* L.). Toinen osajulkaisu tutkii vaihtoehtoisia sydänpuun muodostumisen malleja männyllä. Kolmas osajulkaisu esittää parannuksen latvuksen säteilyolosuhteiden laskentaan perustuen puun rakenneosien keskinäiseen varjostukseen. Neljäs osajulkaisu soveltaa LIGNUM-mallia lehtipuille simuloiden nuoren sokerivaahteran (*Acer saccharum* Marsh) kehitystä. Viides osajulkaisu tuo malliin Lindenmayerin järjestelmät, joilla voidaan määrittää puun arkkitehtuurin kehitystä.

Puun elintoimintoihin perustuvien prosessimallien keskeinen ongelma on ollut ravinteidenoton ja yhteyttämistuotteiden allokaation määrittäminen dynaamisesti kasvavassa puuussa. Tämän väitöskirjan päätulos on esittää ratkaisu, kuinka puun yhteyttämistuotteet jaetaan jopa tuhansien latvuksen muodostavien rakenneosien välillä. LIGNUM-mallilla on mahdollista simuloida puun kolmiulotteisen arkkitehtuurin kehitys, määrittää jokaisen rakenneyksikön kyvyn tuottaa ja kuluttaa resursseja sekä kuvata niiden keskinäiset vuorovaikutukset ja vasteet ympäristölle.

Avainsanat: Rakenteen ja toiminnan malli, puun fysiologia ja arkkitehtuuri, Lindenmayerin järjestelmät, kasvun allokaatio.

Academic dissertation

Systems Analysis Laboratory
Department of Mathematics and Systems Analysis
Helsinki University of Technology

The LIGNUM functional-structural tree model

Author:	Jari Perttunen
Supervising professor:	Prof. Raimo P. Hämäläinen, Helsinki University of Technology
Supervisors:	Dr. Tech. Risto Sievänen, Finnish Forest Research Institute Prof. Eero Nikinmaa, University of Helsinki
Preliminary examiners:	Prof. Pertti Hari, University of Helsinki Dr. Philippe de Reffye, The French National Institute for Research in Computer Science and Control (INRIA), France
Official opponent:	Dr. Christophe Godin, The French National Institute for Research in Computer Science and Control (INRIA), France

Publications

The thesis consists of the accompanying summary article and the following papers:

[I] J. Perttunen, R. Sievänen, E. Nikinmaa, H. Salminen, H. Saarenmaa and J. Väkevä. 1996. LIGNUM: A Tree Model Based on Simple Structural Units. Annals of Botany 77:87-98.

[II] R. Sievänen, E. Nikinmaa and J. Perttunen. 1997. Evaluation of importance of sapwood senescence on tree growth using the model LIGNUM. Silva Fennica 31(3): 329-340.

[III] J. Perttunen, R. Sievänen and E. Nikinmaa. 1998. LIGNUM: a model combining the structure and the functioning of trees. Ecological Modelling 108:189-198.

[IV] J. Perttunen, E. Nikinmaa, M.J. Lechowicz, R. Sievänen and C. Messier. 2001. Application of the Functional-Structural Tree Model LIGNUM to Sugar Maple Saplings (*Acer saccharum* Marsh) Growing in Forest Gaps. Annals of Botany 88:471-481.

[V] J. Perttunen and R. Sievänen. 2005. Incorporating Lindenmayer systems for architectural development in a functional-structural tree model. Ecological Modelling 181: 479-491.

Contribution of the author in the papers

The author was the principal author of papers [I],[III],[IV] and [V], and the author made a notable contribution in paper [II]. Additionally:

[I] The main ideas of developing a tree model consisting of simple structural units was initiated and the model designed collaboratively by the author and the co-authors. The author designed the computer algorithms and programmed the LIGNUM model for Scots pine, carried out most of the simulations and participated actively in analyzing the results and in writing the paper.

[II] The idea to study different formulations of sapwood senescence was initiated by Prof. E. Nikinmaa and Dr. Tech. R. Sievänen. The author implemented the necessary software and participated in carrying out the simulations and analyzing the results and participated in writing the paper.

[III] The modeling work was done collaboratively with Dr. Tech. R. Sievänen. The author implemented the software apart from the model sky based on Ross (1981) which was implemented by Dr. Tech. R. Sievänen. The author carried out the simulations and had the main responsibility for analyzing the results and in writing the paper.

[IV] The author modified and implemented the model LIGNUM for deciduous trees, applied it to sugar maple saplings, carried out the simulations and had the main responsibility in analyzing the results and in writing.

[V] The author initiated the idea to incorporate Lindenmayer systems into LIGNUM. The overall design was a joint effort. The author designed and programmed the algorithms to convert tree structures generated by the Lindenmayer system to LIGNUM and backwards and demonstrated the feasibility of the approach with Scots pine and bearberry. The author had the main responsibility for writing the paper.

Acknowledgements

Prof. Eero Nikinmaa and Dr. Tech. Risto Sievänen, for the support from the very beginning of the LIGNUM model. Without you this thesis would never have been completed.

Prof. Raimo P. Hämäläinen for the welcoming me to your laboratory with the LIGNUM model and for all the support during this work.

Prof. Christian Messier and Prof. Martin Lechowicz, for the possibility to visit UQAM in Montreal on several occasions and to apply the LIGNUM to sugar maple.

Prof. Przemyslaw Prusinkiewicz, for the hospitality during my visit in the Dept. of Computer Science in Calgary and for the opportunity to familiarize myself with the world of Lindenmayer systems.

Prof. Pertti Hari and Dr. Philippe de Reffye for the useful comments on the summary part of the thesis.

Dr. Maija Salemaa for the collaboration with dwarf shrubs.

Lic.Sc. Minna Terho for the collaboration with urban trees.

Dr. John Derome for proof-reading and correcting the text of the summary part of the thesis.

I gratefully acknowledge Emil Aaltonen Foundation and the Foundation for Research of Natural Resources in Finland for their scholarships that supported me in this work.

My sincere thanks to all of you.

We come to know what it means to think when we ourselves try to think.
-Martin Heidegger

Contents

List of Figures

List of Tables

1 Introduction

The functioning of a tree is an activity that captures, processes and allocates resources from the environment. Using the sun's energy, carbon dioxide from the atmosphere and water from the soil, a tree photosynthesizes with its foliage. The rate of this process depends on the local light climate in different parts of the tree crown at a time scale of seconds. The resulting photosynthates are used in processes like growth and respiration in different parts of the tree. Over the years the tree and trees located around it grow thereby altering how the tree experiences and interacts with its environment. The changing environment affects not only the metabolic processes but also how the photosynthates are allocated, thus having an impact on the structure of the tree. The feedback between the structure and functioning of the tree and its interactions with the environment are important factors that need to be taken into account in tree growth modelling (Hari et al., 1982, 1990; Sorrensen-Cothren et al., 1993; Le Roux et al., 2001).

Because a tree can be seen as a hierarchical, dynamic and self-regulating system, its functioning is well suited for studies employing systems analysis methods. A process-based tree model (PBM) is a dynamic model in which the physiology of the tree is derived from the physical and biochemically based processes that take place in the functioning units of interest. For example, a tree can be partitioned into tree crown, stem, branches and root system (Mäkelä, 1997). The model should include how the physiology of the tree is affected by interactions and feedbacks between these units and the environment (Mäkelä et al., 2000). Usually the functioning of the tree is expressed in terms of carbon production and distribution (Mäkelä, 2003) using the differential of difference equations (Landsberg, 1986). Other systems analysis methods such as game theory (Mäkelä, 1985) and optimization (Mäkelä and Sievänen, 1992) have been used to study the height growth strategies of trees.

After thirty years of development the PBMs have become well established scientific tools for capturing, analyzing and understanding the processes governing tree and forest growth (Landsberg, 2003). They are important tools for theory development because a model should not only produce quantitatively realistic results but also act qualitatively in a logical way. The process-based models should finally make predictions about the behaviour of the system under study with limited input regulation. Recently, process-based models have reached a level where they have become of interest for practical forestry (Matala et al., 2003) and have been embedded in user-friendly educational simulation software (Vanninen et al., 2006).

Although a great deal of tree functioning has been clarified using process based tree models, this has been done at the expense of (over)simplified descriptions of tree architecture (Sievänen et al., 2000). It is known that that the three-dimensional crown structure affects, for example, shading and light interception in the tree crown (Sievänen et al., 2000) and the distribution of photosynthates within the tree (Nikinmaa, 1992). The feedback effects which these processes have on the development of the individual organs of trees (Sievänen et al., 2000) have not been considered in the classical PBMs (Voss et al., 2007).

Following the work of Honda (1971) methods have been developed to model tree and plant architecture in general. Perhaps the most widely used methods are the Lindenmayer systems (Prusinkiewicz and Lindenmayer, 1990) but other formalisms based on botanical concepts (de Reffye et al., 1997) and multi-scale tree graphs also exist (Godin et al., 1999). These structural or morphological models have found applications, for example, in the three-dimensional rendering of plants (de Reffye and Houllier, 1997; Prusinkiewicz, 2000; Boudon et al., 2006), analyzing the branching system of the tree crown (Dzierzon et al., 2003), modelling mechanical strengths in branches (Fourcaud and Lac, 1996; Ancelin et al., 2004), computing the light interception inside the tree canopy (Knyazikhin et al., 1998), simulation of plant-insect interaction (Kurth and Sloboda, 2001; Hanan et al., 2002), a basis for interactive tools for designing and manipulating highly irregular crown shapes (Boudon et al., 2003) and incorporating a genetic mechanism into the simulation models of plants (Prusinkiewicz et al., 2007a).

The functional-structural tree growth models (FSTM) emerged in the mid 1990's (see Silva Fennica 31(3), 1997 for the first workshop on functional-structural tree models). They unify the descriptions of physiological processes of trees and the representation of their architecture in a single modelling framework. They provide a link between process based growth models that describe the resource acquisition and partition within a tree and architectural models describing the structural dynamics of trees (Fig. 1). The general elements of FSTMs are presented in Sievänen et al. (2000) and in Prusinkiewicz (2004). The most recent developments can be found in Prusinkiewicz et al. (2007b).

FSTMs usually give a detailed description of (at least) the above-ground part of the tree, representing the topology and the geometry of individual plant organs like shoots or internodes, leaves, flowers and buds. Such an approach allows the descriptions of tree-environment interactions and metabolic processes at the level of the organs where they are taking place. For example, light models with detailed FSTMs can be used to calculate the radiative flux received by each organ (Chelle and Andrieu, 2007). The photosynthesis, transpiration or other processes in the tree crown are computed analogously. The resources produced in the tree are allocated to different parts of the tree and to functions such as growth, respiration, reproduction and protection. Importantly, FSTMs allow (implicitly) the feedback of the new tree structure to future resource uptake and distribution.

The LIGNUM functional-structural tree model (Perttunen et al., 1996, [I]) has its roots in process-based modelling and can be easily seen as a logical and perhaps a dedicated continuum of the work done by the research group at the Department of Forest Ecology, University of Helsinki (see e.g. Hari et al., 1982; Mäkelä and Hari, 1986; Nikinmaa, 1992; Sievänen, 1993; Mäkelä, 1997). The LIGNUM model follows the framework presented already in Hari et al. (1982). LIGNUM has a detailed three-dimensional description of an above ground part of the tree with simple structural units called axis, branching point, tree segment and bud comparable with their real world counter parts enabling, for example, the construction of a detailed model of self-shading within a tree crown.

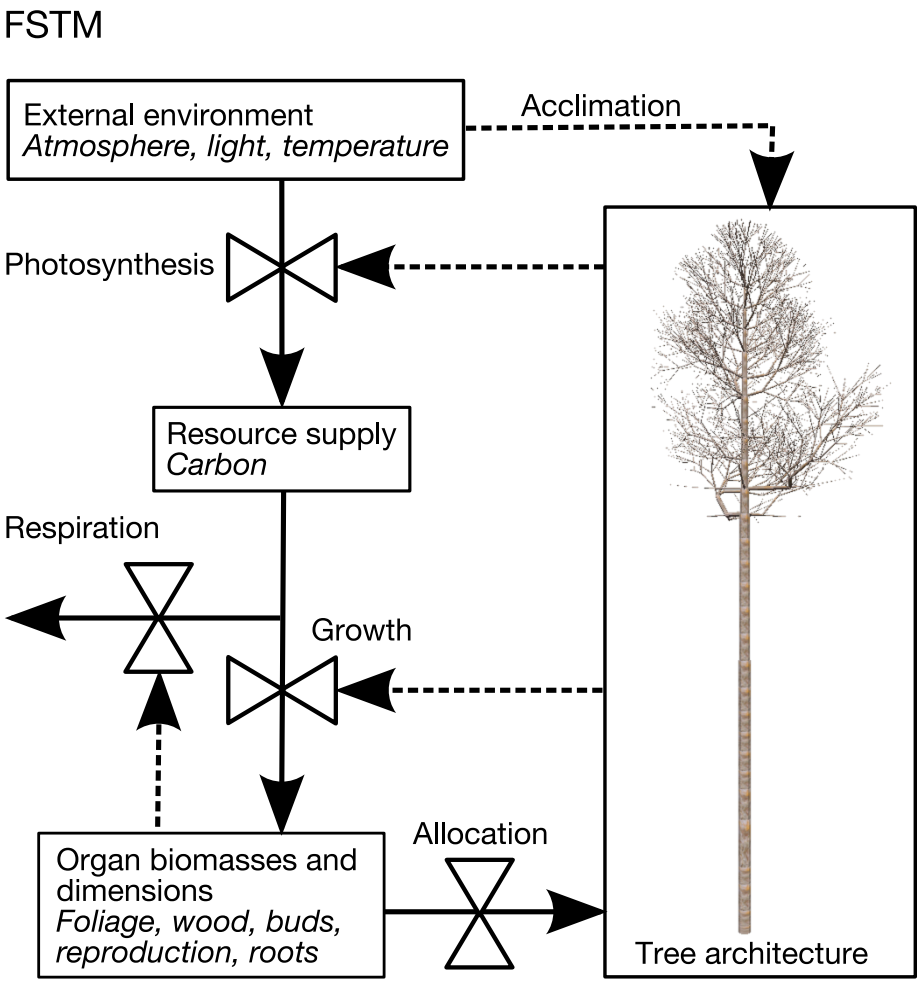


Figure 1: Schematic presentation of a functional-structural tree model (FSTM) in terms of material (carbon) flows (→) and information (⇢) flows. Valves (⋈) represent the metabolic (carbon) processes and boxes (□) the state variables (c.f. Le Roux et al., 2001)

The LIGNUM model has been designed to be a generic modelling tool for woody arborescent plants. It has been applied to coniferous (e.g. Perttunen et al. 1996, [I], Lo et al. 2001) and deciduous trees (e.g. Perttunen et al. 2001, [IV], Lu 2006) as well as to woody clonal dwarf shrubs (Perttunen and Sievänen, 2005, [V]).

The aim of the studies by Perttunen et al. (1996, [I]), Sievänen et al. (1997, [II]), Perttunen et al. (1998, [III]), Perttunen et al. (2001, [IV]) and Perttunen and Sievänen (2005, [V]) which are summarised in this report, has been to construct a single tree model that builds the bridge between traditional PBMs and detailed three-dimensional architectural tree models. The LIGNUM model should deal with resource acquisition and allocation in a dynamically growing tree which has been the central problem of PBMs (Allen et al., 2005). It

should overcome the limitations of traditional empirical partitioning coefficients or functional balance rules that are difficult to apply in trees with multi-year growth because the interactions between resource capture, partitioning, growth and architectural development are too difficult to capture merely with empirical formulae. Instead, the integration of physiological and architectural aspects of tree functioning requires the simulation of the architectural development of a tree crown, while keeping track of each elementary functional unit, defining their local capacity to produce and use resources and determining the interaction with each other and the external environment.

The rest of this summary is organized as follows. Section 2 provides motivation for the construction of FSTMs. Section 3 describes the model structure of LIGNUM. Section 4 addresses the work done in morphological modelling with it, and Section 5 describes its functioning. Section 6 shortly presents three examples to demonstrate questions that can be addressed with FSTMs and finally, in Section 7 the conclusions are made.

2 Functional-structural tree models

Trees like other plants, are modular organisms that are made of and develop through recurring elementary botanical units (Fig. 2). The most basic structural unit is commonly called a metamer or phytomer. It consists of the internode (a segment consisting of layers of xylem, cambium phloem and bark), a node with a leaf or leaves attached to it and axillary buds (Barthélémy and Caraglio, 2007; Sterck and Schieving, 2007). Tree growth is an ordered construction of these botanical entities (Barthélémy and Caraglio, 2007). The production rules for metamers result in species -specific, three-dimensional tree architectures describing the shape and orientation of the structural units in space (Hallé et al., 1978).

An interesting question is how do long lived-trees develop, control and adapt their increasingly complex, three-dimensional architecture to the range of environmental conditions they experience during their life time as they develop from a seedling to a mature tree.

de Reffye et al. (1995) integrated the botanical knowledge (Hallé et al., 1978), measurements of plant structure, and the concept called reference axis (de Reffye et al., 1991) into model plant growth and architecture. A single theoretical reference axis represents the changes in bud functioning, and it describes how the botanical units are assembled in the tree. The rules governing bud fate (growth, branching and mortality) include stochastics and are represented as progressions along this reference axis. For example, AMAPsim (de Reffye et al., 1997) software can produce very realistic three-dimensional models of trees by integrating the results from the simulation of a tree with a reference axis and the geometrical measurements to deduce the position, orientation and size of the botanical units.

The trees produced by AMAPsim are examples of closed systems. There is no interaction between tree growth and the environment. The development

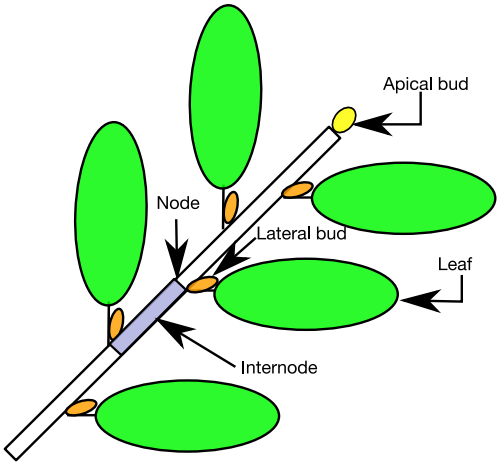


Figure 2: Organisation of a leafy axis or stem. An apical bud is located at the tip of the stem. Each stem consists of a sequence of metamers. A metamer consists of one internode, a node at its tip and accompanying leaf or leaves and the lateral bud.

is self-governing and defined by the reference axis. In contrast, FSTMs describe metabolic processes in the presentation of individual plant organs that are used to represent the three-dimensional structure of the tree. The growth and structural dynamics of the tree are based on the proliferation (bud flush), expansion and senescence of these basic units (Sievänen et al., 2000). Their number, growth rates and sizes are determined by metabolic processes which, in turn, are affected by environmental factors.

In principle there is no limit to which processes and activities (effects of environmental factors, matter exchange with the environment, transport and conversion etc.) could be included in an FSTM. But, as photosynthesis is the process that produces the energy and consequently the material in the tree its description has been the prime interest in FSTMs. Well-known methods exist for assessing the radiation regime in the tree crown or in the canopy (Chelle and Andrieu, 2007) and it is then relatively straightforward to calculate the photosynthetic rates in the foliage. The partitioning of the net photosynthates among competing plant organs has long been an important topic and research problem (see Le Roux et al., 2001; Marcelis and Heuvelink, 2007, for an overview). FSTMs can provide new ways to move forward in modelling the partitioning of carbohydrates in a tree. They allow the modelling of material flows in an explicit three-dimensional crown structure and matter exchange between a tree and its environment.

FSTMs are useful in problems where the explicit three-dimensional spatial struc-

ture of the tree at the organ level is essential when explaining the growth of the tree. Such interesting questions include:

- Resource capture and environment. The assessment of photosynthetic production benefits from a three-dimensional canopy model to simulate light interception (Perttunen et al. 1998, [III]).
- Resource use. Modelling nutrient transport and allocation, hydraulic architecture etc. have to take at least some aspects of branching pattern into account (Le Roux et al., 2001).
- Competition within and between trees. Different tree species have varying morphological possibilities to occupy the growth space. FSTMs can help to understand the benefits and drawbacks of such adaptive options (Brisson, 2001; Cournède et al., 2007).
- Simulating the reproductive and vegetative growth of fruit trees. Developing FSTMs for such species can help to understand the carbon allocation patterns among organs and responses to environmental factors and management practices (Allen et al., 2007).
- Replacing destructive or perhaps impossible experiments and methods, such as calculating the total leaf area of a tree or computing the fractal dimension of a tree crown (Dzierzon et al., 2003).
- In FSTMs root system can follow the same approach as the above-ground part of the tree in accordance with the metamer analogy. Root system studies are needed to make progress in, for example, tree-crop interactions in agroforestry systems, modelling root-mycorrhiza interaction and in developing models of three-dimensional root architecture. Furthermore, three-dimensional models of the below-ground part of the tree provide new forms to analyse the results of the field experiments (Tobin et al., 2007).
- Holistic plant models emphasize the effects of the interactions of functional traits (e.g. carbon allocation, water use, stomatal control) on plant growth, and there is a demand for integrated models that permit the investigation of the interaction of the traits in order to understand biologically complex systems (Marks and Lechowicz, 2006). Functional-structural models may be a common basis for such integrated tree and plant models (Kurth, 1994), because structure or morphology is common to all aspects of plant functioning.

One of the most important objectives in plant modelling is the integration of knowledge. The significance of FSTMs is that they can act as a tool in theory development and serve as a test bed for different hypotheses of tree level phenomena. This can provide interesting research questions for experimental scientists and steer future experiments. And, vice versa, the results from physiological experiments and morphological studies provide new hypothesis and concepts that can be implemented and tested in an FSTM. Importantly, any FSTM should be based on realistic theories of tree functioning and morphology. If this is true, then they can provide the sort of new quantitative insight on tree

growth and development that would not be possible if tree physiology and tree architecture were studied in isolation.

3 The structure of the LIGNUM model

3.1 The representation of a tree

A tree is a woody perennial plant capable of secondary wood growth that has a more or less permanent shoot system. This general concept of trees covers plants ranging from woody dwarf shrubs no more than a few centimeters tall to the tallest living organisms reaching more than a hundred meters in height (Woodward, 2004; Koch et al., 2004). Shrubs are considered as much trees as their larger relative, because they share the same principles in their structural development and metabolic functioning (Thomas, 2000).

LIGNUM is intended to be a generic model for both coniferous and broad-leaved trees (Perttunen et al., 1996, [I], Perttunen et al., 2001, [IV] and Salemaa et al., 2006 as an application of clonal dwarf shrub). Typically when simulating different tree species with LIGNUM, one has to implement models for metabolism, birth, growth (including secondary wood growth) and senescence of structural units, architectural development of the tree and the radiation regime. The main features of the model structure and implementation are presented here in order to understand how LIGNUM is used to model the development of trees.

FSTM's consider the tree in terms of suitable, idealized elementary units that allow both realism in examining the detail and the ability to grasp and understand the whole (Sievänen et al., 2000). They should capture the essential phenomena and neglect the insignificant aspects. The units should be small enough to allow modelling of both the spatial structure and the metabolism of the tree, but at the same time, the number of units must not exceed the computational capacity of the computers.

LIGNUM represents the three-dimensional tree crown by means of four structural units called tree segment (TS), bud (B), branching point (BP) and axis (A). An axis is a sequence of tree segments, branching points and the terminating bud. A branching point is a set of axes, i.e. the position in the tree where one or more tree segments are attached to each other. A tree segment is a section of woody material between two branching points (Fig. 3). The structural units are jointly called tree compartments, and are conceptually similar to the construct of an axial tree, as defined by (Prusinkiewicz and Lindenmayer, 1990).

The cylindrical tree segment consists of dead heartwood, living sapwood and foliage (Fig. 3). It is the main functioning unit of the tree, where the metabolic processes take place and denotes a section of branch or trunk (c.f. Sievänen et al., 2000). Initially, the application for Scots pine (Perttunen et al., 1996, [I]) clearly influenced the choice of units, especially the clear-cut design of the tree segment that corresponds to the annual shoot in conifers.

For hardwood trees the cylindrical layer of foliage was replaced with explicit

leaves (Perttunen et al., 2001, [IV]). A model for a leaf comprises a leaf blade with orientation in space, and a petiole attached to the tree segment at one end and to the leaf blade at the other (Fig. 3). Note also the presence of dormant axillary buds at the axil of each leaf (Perttunen et al., 2001, [IV]).

The form of the leaf blade can be an ellipse (Perttunen et al., 2001, [IV]) or triangle (Lu, 2006). Consequently, the leaf lamina of the species to be modelled only partly covers the leaf ellipse[1], but the choice of simple geometric forms allows us to calculate, for example, irradiance using techniques of elementary computational geometry.

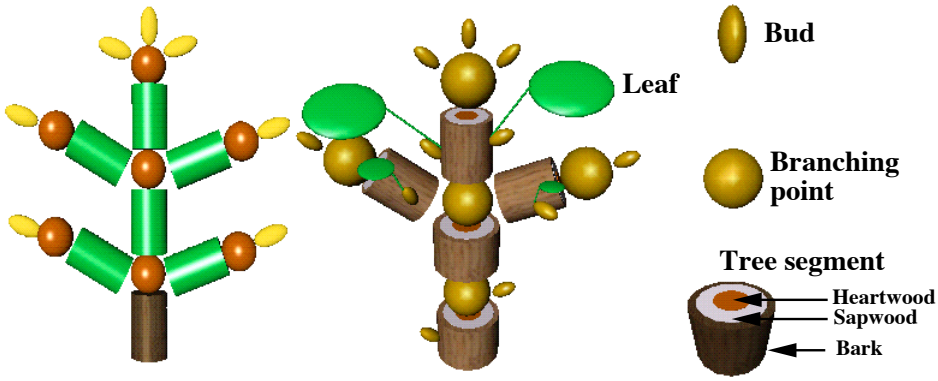


Figure 3: Schematic presentation of a coniferous (left) and broad-leaved tree (centre) using structural units of LIGNUM. Also shown is the structure of a tree segment (bottom right).

The solar radiation is the driving force in modelling tree growth with LIGNUM (Perttunen et al., 1998, [III]). The radiation regime in different parts of the tree crown determines photosynthesis in tree segments (or leaves), each of which experience their own light climate. The availability of photosynthates affects birth and senescence of tree segments and buds (and possibly their orientation in space). The new three-dimensional crown structure affects, in turn, resource capture and the demand for resources in maintaining the structure (i.e. respiration).

3.2 Tree topology

The topological model of a tree, with LIGNUM defining the physical connections between tree compartments, can be stated more formally for example as follows. A tree consists of one (main) axis. The axis is a sequence of tree segments,

[1]See e.g. (Perttunen et al., 2001, [IV]) about how to take care of this inexactness

branching points and the terminating bud. In this sequence each tree segment is followed by one branching point. A branching point is a set of axes.

To illustrate the topological model the axis is represented as a list. Using the list notation adopted in Perttunen et al. (1996, [I]), the main axis for the model for a coniferous tree in Fig. 3 can be written as follows:

$$A = [TS, BP, TS, BP, TS, BP, B] \tag{1}$$

Further, a branching point is a list of axes. When the branching points are unfolded the model tree becomes:

$$A = [TS, [A, A], TS, [A, A], TS, [[B], [B]], B] \tag{2}$$

The purpose of the topological model is to describe the order in which the units appear along the axis: tree segments and branching points alternate and the bud is the last tree compartment terminating the sequence. The recursive structure of the tree crown is captured by the branching point.

The topological model for LIGNUM does not imply that the implementation should be a "list of lists" of tree compartments. For example Dzierzon et al. (2003) implemented converters that translate LIGNUM trees to the data structure of GROGRA (Kurth, 1994, 1999) and to a multi-scale tree graph description of a tree in AMAPmod (Godin and Caraglio, 1998). However, the chosen approach provides a straightforward framework to implement tree models that must include metabolism, insertion and removal of tree compartments, and the architectural development.

Section 4 presents the tree architecture and Section 5 the implementation of physiological processes in LIGNUM.

4 Tree architecture in LIGNUM

Architectural analysis and concepts are of particular importance in understanding the organization and morphological development of plants. Research has established a conceptual and methodological framework for the morphological analysis of plants. A review of the concepts and ideas used in plant architecture and morphology can be found for example in Barthélémy and Caraglio (2007).

4.1 The concept of tree architecture

The fundamental understanding of the tree and plant morphology is due to the seminal work of two European botanists Francis Hallé and Roelof Oldeman. They made a broad comparative study of mainly tropical tree species (Hallé and Oldeman, 1970), and later expanded it to analyse total forest composition (Hallé et al., 1978) by examining the development of trees from seed either in their natural ecosystem or in orchards.

The relatively easily observable features included criteria related to extension growth, branching process, morphological differentiation of the axes and the position of reproductive organs. The features included precise properties such as whether the main stem remains unbranched or not, whether the growth of the tree is seasonal (rythmic vs. continuous growth), and whether the flowering is lateral or terminal, as well as factors representing a continuum of possibilities such as the orientation of branches (Tomlinson, 1983).

Hallé et al. (1978) devised concepts of tree architecture (i.e., a single architectural phase) and architectural model as an abstraction of the genetic blueprint defining the plan of tree growth. The former concept is static, and the latter is dynamic and emphasizes development. Tree architecture is a momentary observable morphological description of the genetic growth plan of the tree. The architectural model for a tree is its genetic growth programme consisting of one or more successive architectural phases.

Originally Hallé and Oldeman found and identified 21 models in tropical rain forests and predicted the existence of three more. One of them was soon found and a new model was added in 1978. Thus the system of Hallé and Oldeman now consists of 23 existing (found) architectural models. The neutral naming system labels each model with the name of an appropriate botanist who has contributed to a study of a tree species belonging to an architectural model rather than that of the tree species itself. The details of each architectural model are given in Hallé and Oldeman (1970) and Hallé et al. (1978).

One should not deduce that each tree can be assigned to exactly one of the named architectural models. A tree may follow an architectural model only when it is a sapling (Bell, 1991) after which other phenomena like accidental events will determine the crown development. Some species share features from more than one model and a tree may achieve its final form through a series of different models(Tomlinson, 1983). However, the surprisingly few 23 models provide universally suitable reference points when studying plant morphology. The system is applicable both to arborescent and to herbaceous plants, from the tropics to temperate regions (Barthélémy and Caraglio, 2007).

4.2 The axial tree

Godin (2000) identifies three types of decomposition information in the morphological models based on the level of detail in decomposition, and geometrical and topological information resolving the complexity of the plant architecture. The global representations (plants as a whole) model plant geometry and topology at a coarse scale use parametric representations of tree crowns such as spheres, cone frustrums or slightly more complex approches like the assymmetric geometric representations introduced by Cescatti (1997). In the more complex modular representations a plant can be viewed to be made up of repeating constructional units of different types and shapes, such as internodes, leaves, flowers or aggregations of these units like branches or sequences of internodes with associated leaves and lateral buds called metamers (Bell, 1991). Thirdly, multi-scale representations further define the hierarchy of the constructional units, i.e. decomposition relationships from one scale to another that superpose

different modular representations in one model, for example, in a multi-scale tree graph (Godin et al., 1999).

Each architectural tree model must address the problem of describing the branching structure dominated in the plant kingdom. Prusinkiewicz and Lindenmayer (1990) proposed a mathematical description for plant modularity based on a graph-theoretical notation called the axial tree. An axial tree represents plants as tree graphs where vertices are the branching points between plant parts and the edges represent the plant components themselves. An axial tree augments the notion for the rooted tree to make a botanically motivated notion of branch segments and axis.

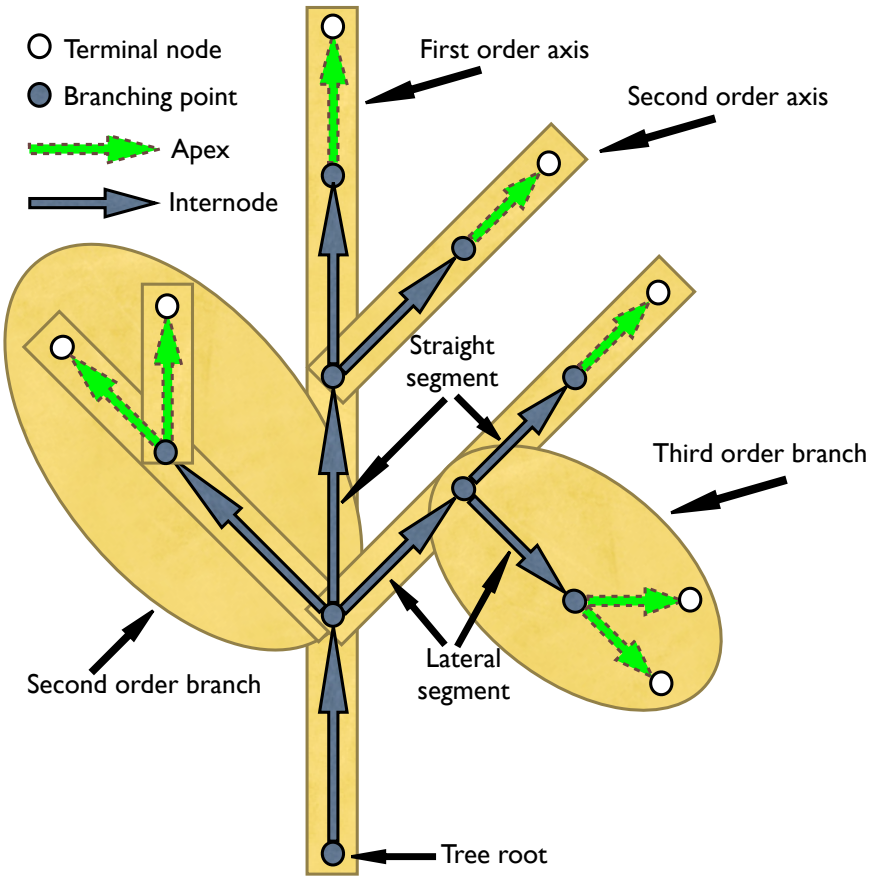


Figure 4: An axial tree according to Prusinkiewicz and Lindenmayer (1990)

More formally, a rooted tree is a tree graph with directed and labelled edges. One vertex is designated as the root. The sequences of edges form paths without cycles from the root. An axial tree is a rooted tree such that, at each vertex, there is at the most one outgoing straight edge, all the other other edges being called lateral. An axis is a sequence of edges if the first edge begins from the root or originates as a lateral from some vertex, each succeeding edge is a straight one, and the last edge is not followed by any straight edge. A branch is an axial

sub-tree, i.e. an axis with all its descendants.

The axes can be numbered by a system introduced originally by Gravelius (1914) as an ordering scheme for river networks. The starting axis from the root of the tree (the main axis) has order one. Axes starting from the main axis have order two. In general, an axis originating from a parent axis of order N has the ordering number N+1.

Axial trees are purely topological, mathematical objects. Importantly, however, they provide the link between the theoretical formalism of a graph and real plant or tree structures for the modelling purposes. One can make the argument that all botanical trees can be expressed with the formalism of axial trees. The definition of an axial tree does not specify how to implement a botanical tree model, but the formalism can be used as a tool for model comparisons.

For example, it is easy to see the close similarity between the model structure of LIGNUM (Fig. 3) and the axial tree (Fig. 4). The tree segment in LIGNUM corresponds to internodes and apices in axial tree, buds to terminal nodes, and both identify branching points.

4.3 Computer simulation of tree architecture

The complex modular architecture of trees and plants, their diversity and plasticity, i.e. the ability of plants to adapt to their environment, has attracted plant scientists, mathematicians, computer scientists etc. to find methods to capture this variety in a unified and universally concise way.

The first computer simulations that modelled branching patterns and tree form appeared contemporary with the evolvement of the 'French school' of tree architecture. Before that the botanical drawings were the only way to illustrate plant or tree architecture. The pioneering work was performed by Honda (1971), who devised a model to simulate the crown shape of trees with a only a few parameters describing the repeated bifurcation of branches.

Fisher and Honda (1977) refined the original approach of Honda (1971), and introduced a model having more detailed rules for the growth of the main axis of the tree and lateral branching to produce the first computer simulations of architectural models by Hallé et al. (1978). The results by Fisher and Honda (1977) showed that very little geometric information about branching angles and branch lengths could produce realistic tree crowns. Importantly, small changes in the parameter values could produce a wide variety of distinctive crown shapes and the final crown geometry was difficult to predict.

This pioneering work started a vibrant phase of interdisciplinary work on plant architecture modelling, and the last few decades have produced (along with the development of computers) a variety of formal representations of plant architecture, including strings of characters, tree graphs, multi-scale graphs, list of lists, matrices, fractals etc. The proposed representation is motivated by providing efficient computational properties in terms of computing time, storage use for the problem or the ease of expressing the mathematical equations. For example, Fourcaud and Lac (1996) used a matrix representation to apply efficiently the

finite element method in the mechanical stress analysis of stem and branches to model the development of a tree shape using the righting movement of a tilted Maritime pine to an upright position.

Although there have been a multitude of approaches, two important formalisms can be identified that have evolved and produced software tools to describe and understand the mechanisms of how trees and plants acquire, in general, their form.

An important theoretical framework based on term rewriting systems was introduced by the Hungarian botanist, Aristid Lindenmayer (1968), to simulate the development of simple multi-cellular organisms. His approach was later named the Lindenmayer systems or L systems for short. This formalism was closely related to formal languages, and in essence it views the plant development as a parallel rewriting system.

In L systems a plant is viewed as an assembly of discrete modules. A module represents any constructional unit in a plant that is repeated as the plant develops, such as an internode, a bud (apical meristem), a leaf or a flower (Prusinkiewicz et al., 1997). L systems are dynamic, i.e. the shape and state of an organism is the result of development, not its static 'snapshot' configuration in space. The rewriting rules can change the state of a module, replace it with new modules, or remove it from the plant structure.

Over the years the development of the theory of L systems has gradually extended the formalism to expand the range of phenomena that can be included in plant modelling. For example, context free L systems (Prusinkiewicz et al., 1997) can describe the transfer of information from a parent module to its progeny (lineage). The communication between adjacent plant parts and the propagation of information through the growing plant structure (endogenous interaction) can be performed with context-sensitive L systems (Prusinkiewicz et al., 1997). An important extension was the incorporation of communication modules (Prusinkiewicz, 1999) or predefined functions (Kurth, 1994), which allow information transfer between the plant and its environment (exogenous interaction). See Prusinkiewicz and Lindenmayer (1990) and Kurth (1999) for the development up until the end of the 1990's.

Recently the L+C language (Karwowski and Prusinkiewicz, 2003; Prusinkiewicz et al., 2007c) has embedded the programming language C++ with an L system based language that allows fast (linear time) information flow within a plant. The XL language implements a relational growth grammar (Kurth et al., 2005), and a graph rewriting system, which generalises and extends L systems formalisms from a linear sequence of modules to a network of modules represented as a graph.

L systems and their extensions known as growth grammars (Kurth, 1994) have been applied in various studies on higher plants, for example, plant-insect interaction (Kurth and Sloboda, 2001; Hanan et al., 2002) the development of boreal shrubs in different environmental conditions (Salemaa and Sievänen, 2002), and the tree architecture of grafted stone pine (Mutke et al., 2005).

Morphological algorithms (e.g. fractals), L systems and associated modelling

tools (Kurth, 1994; Prusinkiewicz et al., 2007c; Kniemeyer et al., 2007) are not the only possibility to model plant architecture and morphology. The AMAP[2] approach initiated by Philipe de Reffye in the early 1980's with coffee plant emphasizes the correct and detailed botanical description of plants.

The central assumption of the AMAP approach is that the plant structure at any given time is the result of a species-specific morphogenetic programme (de Reffye and Houllier, 1997; Hallé et al., 1978) and the physiological processes. Furthermore, the importance of feedback between the plant structure and its functioning and the environment is recognised (de Reffye et al., 1997). The AMAP approach has been put into practice as a set of software tools.

Static three-dimensional architectural models for plants derived from field measurements can be generated, visualised and explored with AMAPmod (de Reffye et al., 1995). The software is based on a hierarchical representation of a plant using the formalism of multi-scale tree graphs (Godin and Caraglio, 1998) and stochastic branching models based on experimental data. It has a querying language (called AML) for exploring the organisation of the plant, for example, the number of internodes in a growth unit.

AMAPsim (de Reffye et al., 1997) can be used to simulate the architectural development of plants (as closed systems) with so-called reference axis techniques (Blaise et al., 1998). The one-dimensional reference axis is a theoretical plant axis that captures the branching process and the different developmental states of buds (apical meristem) in a plant from birth to maturity. The progression along the reference axis implies the physiological ageing of the bud, i.e. the type of elementary growth units or botanical units it produces. The reference axis is simulated with a finite automaton that gives transition probabilities (based on measurements) from one developmental state to another. AMAPsim is connected to AMAPmod; there is a direct link between plant architectural measurements and simulations of the morphological characteristics of plants.

The AMAP family of software is an example of how functional structural models can be achieved by adding plant physiology to a detailed architectural model (c.f. Sievänen et al., 2000). AMAPpara (de Reffye et al., 1997) can simulate the parallel growth of plants interacting with each other, while also taking into account the resources produced and used by the physiological processes. The topology, geometry, allometric relationships for growth units and the morphogenetic programme of the plant are predefined (c.f. AMAPsim) and species specific, but the actual growth and development is an interplay between physiological processes, physical constraints and the existing tree architecture.

The recent GreenLab initiative (de Reffye and Hu, 2003; de Reffye and Cournède, 2005) carries on the AMAP approach of botanically faithful plant models but introduces a new mathematical model, factorisation algorithm, to simulate functional structural models in a computationally effective manner. Due to the factorisation algorithm, the plant (tree) is divided into substructures that can be represented repeatedly in the model structure (Yan et al., 2004). In addition, it is possible (at least to some extent) to study the model behaviour analytically.

[2] botAnique et bioinforMatique de l'Architecture des Plantes, Cirad, France

4.4 Lindenmayer systems in LIGNUM

The LIGNUM tree model has a list representation (Section 3.2) for the branching structure of trees that is implemented with a general purpose programming language. Both the metabolic processes and the crown development were implemented with C++ (Stroustrup, 1997). Perttunen and Sievänen (2005, [V]) introduced the use of L systems (Prusinkiewicz and Lindenmayer, 1990) using the L language (Prusinkiewicz et al., 1999) within LIGNUM for the architectural development of a tree structure. Applying the language L was motivated by the observation of the close likeness in how bracketed L systems[3] (Lindenmayer, 1968) represent the branching structure of trees and provide a data structure for implementing axial tree.

Mathematically the L systems are parallel rewriting systems that operate on sequences of symbols. An L system is defined by an alphabet of symbols, a set of rewriting rules called productions, each rule substituting a symbol 'a' for a sequence 's'. The rewriting starts from an initial string called an axiom. In the plant modelling context the symbols in the alphabet represent the units of the growing plant, for example, internodes, buds, leaves and flowers, and the sequence of symbols their topological ordering.

In the L language the symbols are called modules. A module has a name and it can take any number of arguments of any type allowed in C++ programming language. A rule in L consists of a predecessor module, its optional context, and a production defining the sequence of modules replacing the predecessor. A special module Start is dedicated to correspond to the axiom.

To demonstrate the rewriting in L systems let us define a simple context free L system in L consisting of two modules A() and B() and the set of two rules:

$$Start() : produceA();$$
$$A() : produceB()A();$$
$$B() : produceA()B();$$

Starting from the axiom A() the first four sequences of symbols produced are A(), B()A(), A()B()B()A(), B()A()A()B()A()B()B()A(). Note the parallel rewriting.

To model tree structures with L as in LIGNUM (Section 3.2), let the module F denote a tree segment and assign the module B for a bud. For branching structures L has two modules SB() and EB(), denoting the beginning and the end of a branch, respectively. An L system for the development of crown architecture resembling a young Scots pine implemented in the language L is listed in Appendix B. The symbols and their meanings in the L system are:

[3]Denoting the beginning and the end of an branch literally with '[' and ']' respectively

Start() the axiom

F(s) produce a tree segment of length s

B(g,l) produce a bud with Gravelius order g and the length of the segment produced by the bud is l

SB() start of a branching point

EB() end of a branching point

Pitch(α) change the growth direction downwards or upwards

Roll(α) change the growth direction by turning over

Turn(α) change the growth direction to the left or to the right.

Bend(α) gradual bending of branches

Development starts from one tree segment and the terminating bud. During one iteration or rewriting of the L system, the main axis produces one segment and four side branches of Gravelius order 2. Each side branch of order 2 and 3 produce one segment and two side branches. The branching stops in order 4, but the fourth order branches continue their growth. The gradual bending of branches is implemented by revising the growth direction of second order branches gradually downwards. The crown architecture produced by the L system without metabolism after eight iterations is given in Section 6.1, Fig. 5(a).

The geometrical interpretation of the L system string can be performed in many ways. To translate the L string to a LIGNUM structure (and vice versa) a LOGO like turtle (Abelson and di Sesa, 1982) has been implemented for the turtle interpretation of L systems (Prusinkiewicz, 1986). Turtle's place and orientation in space is defined by three unit vectors $\vec{H}$, $\vec{L}$ and $\vec{U}$ denoting the heading (i.e. forward direction), direction to the left and up respectively so that $\vec{U} = \vec{H} \times \vec{L}$. The module F(s) moves the turtle forward along its heading of length s, and the rotations of the turtle by three modules Turn(α), Pitch(α), Roll(α) to rotate the turtle around $\vec{U}$, $\vec{L}$ and $\vec{H}$, respectively, by angle α.

After the L string is created it is scanned from left to right and the symbols are interpreted as commands to steer the turtle. Given the state of the turtle and matching the modules F and B with corresponding tree segments and buds in the LIGNUM data structure, the position and orientation of tree segments and buds in space can be defined during the scan. The algorithms that translate L system strings into a LIGNUM data structure and vice versa, including a two-way communication mechanism to pass information between the two, are described in Perttunen and Sievänen (2005, [V]). The final dimensions of the tree segments are resolved by the metabolic processes (see Section 5). The original parser for the L language was written by R. Karwowski, who has more recently implemented the L+C language (Karwowski, 2002).

The use of the L language in LIGNUM can be seen as an example of convergence between different architectural plant models. Already (Kurth, 1994) described

how morphological models constructed by AMAP can be formalised by extending L systems with notion stochastic growth grammars. Ferraro et al. (2002) reported algorithms converting plant structures generated by L systems into the multi-scale tree graphs introduced by Godin and Caraglio (1998). Dzierzon et al. (2003) reported a data interface between LIGNUM and the L system based software system GROGRA. The implementation for connecting LIGNUM to AMAPmod database (Godin et al., 1997) is described in Dzierzon and Kurth (2002).

5 Tree functioning in LIGNUM

Tree growth is a matter of allocation or partitioning of photosynthetically fixed carbon. The main processes to consider are the assimilation of carbon in photosynthesis, respiration through which carbon is lost back to the atmosphere, senescence of living biomass, and the allocation of growth into new and existing component parts of the tree, for example, sapwood and bark in stems and branches, foliage and roots.

The share of carbon that is allocated to various parts of the tree will determine the growth pattern of the tree, the capacity for future growth in different tree parts, and the ability of the tree to respond to environmental stresses. Carbon allocation has been the subject of intensive studies (see Section 5.4). One of the most difficult aspects and which is still an open research problem in FSTMs (Allen et al., 2005), has been to develop mechanisms to explain how carbon allocation responds to environmental factors and to describe the interactions between carbon partitioning, growth and architecture in dynamically growing, perennial plants with multiyear growth. The ability to explain and predict tree growth and its responses to disturbances and management practices depends on how well the mechanisms affecting carbon allocation are understood.

An important methodological problem in LIGNUM is how to subsume the carbon balance, i.e. allocation of the net photosynthates, in a model consisting of a large number of units. In evaluating the growth increment, photosynthesis (P) and respiration (M) are first summed up for the whole tree. If the photosynthetic production exceeds the respirational costs for foliage, sapwood and roots, then the tree can extend its branches by adding new segments, ΔW_n, thicken existing segments, ΔW_o, and add new roots ΔW_r. At the tree level, the carbon balance in LIGNUM can be formulated as:

$$P - M = \Delta W_n + \Delta W_o + \Delta W_r \quad \text{and} \quad P - M > 0 \tag{3}$$

The components of the carbon balance (Eq. 3) in LIGNUM are presented in Sections 5.1 – 5.4.

5.1 Modelling photosynthesis

The light interception of the tree crown depends on the incident solar radiation[4] at the top of the tree or forest canopy, the optical properties of the structural units of the tree, their arrangement in the tree crown (clumping) and the tree architecture. The most important component of the tree crown regarding light interception and photosynthesis is foliage. Leaves and needles intercept radiation, attenuate or reduce its force (i.e. shading) and, finally, convert radiation into carbohydrates in photosynthesis.

FSTMs can provide explicit three-dimensional descriptions of a tree crown in order to quantitatively describe how the solar radiation acts within the tree crown. Many radiative transfer models have been developed at a number of levels of structural detail (shoot level, tree level, layers of foliage etc.) and degrees of complexity, for example, accounting for the light reflection in tree crown (Chelle and Andrieu, 2007).

Photosynthesis has been, and still is, a subject of intense study and a lot of ecophysiological research has been devoted to the experimental and modelling work because it is considered to be the fundamental biological process (Landsberg and Gower, 1997). Our knowledge of the processes involved in photosynthesis is satisfactory, and species-specific parameters for the photosynthesis models can be obtained with commercially available portable measuring devices. Three different approaches or model families can be identified with respect to the photosynthesis formulation: implicit, empirical and biochemically based models (Sinoquet and Roux, 2000).

However, photosynthesis is only the first in a series of processes that results in the growth of the tree. It is probably safe to say that insufficient understanding of the mechanisms involved in carbon allocation is the major obstacle and research problem in developing the functional part of FSTMs.

5.1.1 Implicit photosynthesis models

Implicit photosynthesis models compute the photosynthetic rate or carbon uptake, P, as proportional to the unshaded photosynthetic rate, ρ, shading, f, of the foliage mass or area, w_f, and the area or mass (A_f, W_f) of the photosynthesising foliage (e.g. Mäkelä and Hari, 1986; Deleuze and Houllier, 1995; Mäkelä, 1997):

$$P = \rho f(w_f) A_f \qquad \text{or} \qquad P = \rho f(w_f) W_f \tag{4}$$

The unit of measurement for P is the amount of carbon per time unit, for example $kgC\ year^{-1}$.

A slightly different approach is used in the model developed by de Reffye et al. (1997). It has a detailed description of tree hydraulic architecture and can compute water fluxes. The coupling between water fluxes and P is assumed to be proportional to transpiration E:

$$P = \mathrm{WUE} E \tag{5}$$

[4]The total radiation on a specific surface area over a specific time interval

where WUE is the water use efficiency.

The models using the first approach (Eq. 4, 5) assume that the plant production, based on intercepted PAR, leaf area, leaf mass or transpiration, is constant within the tree crown. The time step in these models is generally one year, i.e. the photosynthesis parameter represents an aggregate value over the growing season, although it can depend for example on tree age (Sorrensen-Cothren et al., 1993) or be modified by tree height (Mäkelä, 1997).

5.1.2 Empirical photosynthesis models

A second group of models for simulating the foliage photosynthesis are based on functional relationships that describe the responsiveness to certain environmental conditions and the parameters are fitted on the basis of empirical findings. Typically such photosynthesis models include the multiplicative elements in Eq. 6 (from Le Roux et al., 2001):

$$\begin{aligned} \mathrm{P} = P_{\max} f(\mathrm{PAR}) g_1(T) g_2(CO_2) \\ g_3(\mathrm{VPD}) g_4(\Psi) g_5(N) g_6(\mathrm{age}) \end{aligned} \tag{6}$$

$P_{\max}$ is measured at optimal conditions in high leaf irradiance and represents the maximum photosynthetic rate. $f(\mathrm{PAR})$ is the essential empirical saturating function for the effect of leaf irradiance. According to Le Roux et al. (2001), the most common functions used are rectangular (Host et al., 1990; Zhang et al., 1994) or non rectangular hyperbolae (Thornley, 1991; Grossmann and DeJong, 1994; Sterck et al., 2005). The g_i's stand for the effects of air temperature, air CO_2 concentration, air water vapor pressure deficit (VPD), water potential (Ψ), leaf nitrogen concentration (N) and leaf age.

5.1.3 Biochemically based photosynthesis models

Leaf photosynthesis responds instantaneously to the environmental characteristics such as temperature, radiation regime or irradiance experienced by the foliage and CO_2 concentration in the air. The biochemically based photosynthesis model for C3 plants[5] was originally described by Farquhar et al. (1980) and it accounts for the effects of major environmental variables on the leaf photosynthesis. The model describes the photosynthetic rate as a function of leaf irradiance, the intercellular CO_2 partial pressure in the leaf, and the leaf temperature. A comprehensive treatment of the photosynthesis model of Farquhar et al. (1980) and the development of the two less used models for C4 and C3-C4 plants can be found in von Caemmerer (2000).

There are many ways in which a biochemically based photosynthesis model can be constructed (von Caemmerer, 2000). Each of them provides a set of assump-

[5]Plant metabolism can be divided into three categories – C3, C4 and the unusual C3-C4 – based on the way in which they assimilate carbon dioxide in early stages of photosynthesis. C3-type plants, including trees, form more than 95% of the plant biomass of the earth; C4 plants, mainly tropical species, account for about 20% of global carbon fixationvon Caemmerer (2000)

tions or hypothesis and formulates them in quantitative numerical form. The model by Farquhar et al. (1980) is considered as one of the most authoritative (Le Roux et al., 2001) and it is widely used with many modifications (see Cheeseman and Lexa (1996) for a review). These biochemically based models (as well as the empirical models) permit the modelling of photosynthesis in very small time steps of one hour or less (Le Roux et al., 2001). This allows the modelling of fast-growing tree species which have several structural updates during a growing season, i.e. when aggregate photosynthesis models are not applicable to model the development of the tree.

The LIGNUM model has been applied to simulate short-rotation eastern cottonwood (*Populus deltoides* Bartr. ex Marsh.) in Lu (2006). The adaptation makes the use of the basic modelling concepts such as the representation of the tree structure, Lindenmayer systems to define the architectural development, and the carbon allocation scheme. In order to model this fast growing species a CO_2 exchange model for leaf photosynthesis was applied based on Farquhar's approach (von Caemmerer and Farquhar, 1981; Long, 1991; Le Roux et al., 1999). Photosynthesis in the eastern cottonwood model was computed in a 30-minutes time step and the net assimilates were allocated to structural growth several times within one growing season.

5.2 Radiation regime and photosynthesis in LIGNUM

In the LIGNUM model the amount of photosynthetically active radiation (PAR) during the growing period is the critical environmental input used in assessing the photosynthesis of the tree. For this purpose a model sky has been implemented in which the hemisphere is divided into sectors of approximately solid angles. The incoming radiation originates from the midpoint of each sector by applying the standard overcast sky radiation (SOC) distribution (Ross, 1981). The number of inclinations and azimuthal directions can be altered in order to define the number of sky sectors. The total incoming radiation at the horizontal plane above the forest canopy can also be adjusted according to data available for the geographic location of interest (Perttunen et al. 1998, [III], Perttunen et al. 2001, [IV]. See also Sections 6.1, 6.2.1 and 6.2.2).

In LIGNUM the intercepted or absorbed radiation in different parts of the tree crown has been based on (mutual) shading of the photosynthesizing elements. In other words, calculating the self shading within the tree crown is the basic process applied in assessing photosynthetic production. The photosynthesis P in a coniferous segment (Perttunen et al. (1998, [III]),Lo et al. (2001)) or in a leaf (Perttunen et al., 2001, [IV]) is then assumed to be directly proportional to the amount of approximated intercepted radiation at the annual level or growing season, i.e.:

$$P = \eta_c \times I \tag{7}$$

where η_c is an empirically determined parameter. For the whole tree the production is simply the sum of the photosynthesis that has taken place in all the segments.

In the case of conifers, the shading elements are cylindrical tree segments (Pert-

tunen et al., 1998, [III]) and the geometrical problem is to compute the entry and exit points of a line through the cylinder (Rogers and Alan, 1990), i.e. the distance a light ray traverses in shading foliage or if it hits the woody part of a segment, thus blocking the light coming from that sector. In the case of hardwoods the shading elements are ellipsical (Perttunen et al., 2001, [IV]) or triangular shaped (Lu, 2006) leaves, and the problem is to check whether a line intersects an ellipse or triangle positioned in three-dimensional space (Hearn and Baker, 1994).

Suppose the distance a light ray has traversed in the foliage of one segment is l. Based on the results of Oker-Blom and Smolander (1988), the transmission h of the light beam through one segment is:

$$h = \exp^{-K(\phi)(A_f/V_f)l} \tag{8}$$

where A_f and V_f are the foliage area (by folding out the cylindrical layer foliage to a rectangular shape) and the volume occupied by the foliage, respectively, K is the empirically determined function (Oker-Blom and Smolander, 1988) defining the light extinction coefficient as a function of its elevation angle. The proportion of radiant energy passing through all N shading segments is $H = \prod_N h_i$, and the radiant energy reaching the shaded segment from one sector $I = HI_0$, where I_0 is the radiant intensity of the sky sector that the light beam represents,.

The amount of radiation intercepted by the target segment s from one sky sector depends on its foliage area and its projection area A_C in the direction of the light beam:

$$I_s = (1 - exp^{-K(\phi)A_f/A_C})A_C I \tag{9}$$

adopted from Kellomäki and Strandman (1995), When the angle ϕ between the segment axis and the light beam is known A_C is given by Oker-Blom and Smolander (1988)

$$A_C = 2LR\cos(\phi) + \pi R^2 \sin(\phi) \tag{10}$$

where L and R are the segment length and radius respectively. The total amount of radiation intercepted by the segment is the sum of the results in Eq. 9 from each sky sector.

The calculations for the intercepted radiation are easier in the case of broadleaf trees. The transmission through one leaf is assumed to be

$$h = 1 - d_f + d_f(1 - \nu) \tag{11}$$

where ν is the attenuation and the term $d_f (d_f \leq 1)$ describes how well the actual leaf of the tree species fills the selected shape, an ellipse or a triangle (c.f. 3.1).

Analogous to conifers, the radiant energy coming from one sky sector is $H = \prod_N h$, where N is the number of leaves on the path of the light ray. The radiant energy from one sector reaching the shaded leaf is $I = HI_0$, and the amount of intercepted radiation I_s depends on the angle of incidence α of the light ray on the leaf:

$$I_s = I\cos(\alpha)A_l \tag{12}$$

where A_l is the leaf area. As with conifers, the total absorbed radiation is the summation of the irradiances I_s over all sky sectors.

5.3 Respiration

5.3.1 Modelling respiration

The respiration losses affect the net production of plant biomass. In temperate forests, for example, the respiration losses may be 40 % - 60 % of total gross photosynthesis (Sprugel and Benecke, 1991). There seems to be general agreement that plant respiration consists of two components. Growth respiration takes place during the formation of new biomass, and maintenance respiration provides energy for preserving the existing biomass. (Thornley, 1970). Most tree growth models use the two-component representation of respiration; some calculate the maintenance respiration only or use a global, implicit treatment for respiratory processes (Le Roux et al., 2001).

In the two-component models, the work carried out by either McCree (1970) or Thornley (1970) is commonly used as the theoretical framework to split the total respiration into growth and maintenance components. The simple equation by McCree (1970) describes the behaviour of the whole plant using the relationships between photosynthesis and respiration:

$$R_t = kP + cW \tag{13}$$

where R_t is the total respiration, P photosynthesis and W the living, respiring plant (dry) weight. The constants k and c are related to growth and maintenance, respectively, such that kP is growth respiration and cW is maintenance respiration.

Thornley (1970) assumes that the photosynthates, P, produced during the time interval in question are fully utilized in either maintenance,R_M, or new growth, G, i.e. there is no change in the amount of storage material. Part of the new growth is respired, R_G, and a part is used for new structure, ΔW:

$$P = R_M + G \qquad \text{and} \qquad G = R_G + \Delta W \tag{14}$$

In the total respiration, R_T, the maintenance is assumed to be proportional to the living biomass:

$$R_T = R_G + R_M \qquad \text{and} \qquad R_M = mW \tag{15}$$

Thornley (1970) further introduced the idea of yield, Y_G being defined as the ratio of new structural matter, ΔW, to the total amount of assimilates required for growth:

$$Y_G = \frac{\Delta W}{R_G + \Delta W} \tag{16}$$

By denoting $R_G + R_M = P - \Delta W$, solving for ΔW in Eq. 16, and applying the results in Eq. 15, one can obtain Thornley's decomposition to R_T (Thornley, 1970) :

$$R_T = (1 - Y_G)P + mY_GW \tag{17}$$

which has the same form as in Eq. 13.

The growth models appear to use Thornley's formulation (Le Roux et al., 2001), while only a few models running at an annual time step (e.g. Deleuze and Houllier, 1995; Zhang et al., 1994) use the McCree formulation(McCree, 1970).

It should be noted that, although of the same form, the growth and maintenance respiration components are not the same in Eqs. 13 and 17. The choice of the model for R_G as a function of photosynthesis or growth determines the type of coefficient for R_M. When deriving respiration coefficients from the literature (as most growth models do), incompatibilities in the formulations of the respiration components can result in significant errors in R_T (Le Roux et al., 2001).

5.3.2 Modelling respiration in LIGNUM

The LIGNUM model has used the one-component approach, i.e., maintenance respiration R_M is calculated as a function of the weight of living tissue W in each tree segment and in the aggregated root system

$$R_{M_i} = k_i W_i \tag{18}$$

with a different coefficient k_i for the foliage, sapwood and roots. After accounting for the respiration costs the net photosynthesis is allocated to new growth (see Section 5.4). Other examples of the one-component approach are the models by Takenaka (1994) for leaf maintenance respiration and by Prentice et al. (1993) for sapwood maintenance respiration.

5.4 Allocation of photosynthates

The allocation of assimilates is an indispensable and all-important part of every FSTM. Carbon allocation and growth cannot be separated. In the short term, partitioning the available photosynthates in different tree parts and in their metabolism governs the relative growth of these components. In the long term, the numerous feedback processes in assimilate allocation makes it even more important.

Numerous studies (Lacointe, 2000) have been carried out on formulation of the allocation of assimilates in trees, and some general features can be identified. Five main techniques have been used to allocate photosynthates in trees:

- Empirical allocation models
- Transport-resistance models
- Source-sink models
- Descriptive allometric relationships between tree parts
- Functional balance

The allocation of assimilates to the formation of new structure, thereby defining the architecture and geometry of a tree, is affected by the local conditions (e.g.

self shading) in different parts of the tree. This has an impact on the capability of the tree to perform its resource acquisition and storage. Understanding these responses between the gradual accumulation of growth and the metabolic processes taking place over many years is essential in studying the dynamics of tree functioning and structure (Nikinmaa, 1992). It is the central and still an open problem for FSTMs as well as in plant sciences.

5.4.1 Empirical allocation models

Empirical allocation models do not have rules or mechanisms that determine the allocation. Instead, the allocation or partitioning coefficients are based on measurements in order to assign a given part of the available photosynthates to each plant part or organ. One example is the model by Mäkelä and Hari (1986), in which the allocation coefficients are based on the light environment. At the other end of the spectrum of complexity is the carbon allocation and transportation model ECOPHYS design for *Populus* species (Rauscher et al., 1990; Lenz et al., 2004). It has a detailed matrix of allocation coefficients, created on the basis of poplar studies, from each source leaf to the different growth centres in a tree.

The main limitation of the empirical models is that the allocation coefficients can be applied only within a limited range of conditions and must be remeasured for different situations. However, some flexibility can be achieved: the allocation coefficients can be modified according to the external conditions such as photosynthetically active radiation (Mäkelä and Hari, 1986) or soil water potential (Zhang et al., 1994). If the conditions are met then these models are very efficient in simulating tree growth.

5.4.2 Transport-resistance models

The transport-resistance models (TR models) describe the movement of phosynthates (Thornely, 1972). The movement of assimilates is driven by concentration differences along the resistive pathways between the source (leaves) and the sink (e.g. roots). The influential work by Thornley initially proposed a two-substrate TR model Thornely (1972) for shoot-root partitioning in relation to C and N moving in opposite directions. Thornley (1991) demonstrated the feasibility of the approach on a forest stand. However, TR models have not yet found their way to FSTMs (Lacointe, 2000) and, so far, they have been applied in models with little or no tree architecture.

5.4.3 Source-sink models

In the source-sink relationship models the allocation of assimilates is controlled by the ability of sinks to import available photosynthates from sources. Depending on the model-specific implementation, this growth demand or sink strength is also called, for example, the maximum, potential or conditional growth rate. In order to account for feedback effects within a tree or between the environ-

ment and the tree (e.g. Grossmann and DeJong, 1994), the sink strength can be updated at each time step during the simulation.

In the hierarchical source-sink models the different sinks have a priority level or are ordered in the hierarchy, and the sink with the highest priority is satisfied first. Then, as long as there are available assimilates left, the sinks are supplied one after another in the priority level order to meet their requirements. For example, the priority for the growth of tree parts (roots, shoots, fruits) may depend on the height level in the tree or on their proximity to sources (Grossmann and DeJong, 1994).

In the original formulation of proportional source-sink models (Warren-Wilson, 1972), the allocation of assimilates to each sink is defined in proportion to the demand of that sink (not greater than that). This basic approach can be extended to include, for example, distance or affinity between sources and sinks, as in (Balandier et al., 2000).

5.4.4 Descriptive allometric relationships

Models using empirical allometric relationships describe, to a varying extent, the growth patterns in a tree or plant. It is assumed that the size of one plant part, Y can be described on the basis of another part, M. An example of such a relationship is the leaf weight and the supporting branch weight. When using biomasses such relationships can be expressed as:

$$Y = aM^b \tag{19}$$

where a and b are empirical constants determining the relative sizes of the plant parts. However, how constant are the relationships between different parts and over time in different environmental conditions is still an open question. However, models using this approach are rather simple and can explain a relatively high proportion of the internal dynamics of, for example, forest stand (Sievänen et al., 2000).

The pipe model originally developed by Shinozaki et al. (1964) assumes that the water conducting tissue (sapwood) consists of pipes that connect each foliage element to the tip of the roots. Disused pipes that no longer connect to their respective foliage die and form heartwood. Shinozaki et al. (1964) found a linear relationship between the foliage mass, W_f, of a tree and the sapwood cross-sectional area, A, below the crown:

$$\eta = \frac{W_f}{A} \tag{20}$$

where η is the species-specific constant. Mäkelä and Hari (1986) applied this in a photosynthesis-based tree growth model. The constant η is usually assigned different values in different parts of the tree. For example, Mäkelä (1997) has defined one for the main stem, one for branches and one for coarse roots.

Although the real hydraulic network in a tree is not merely a bundle of pipes, empirical work has shown that the pipe model, at least for some tree species,

can explain the relationship between foliage and wood growth. It is one of the most used and cited present-day models of whole plants and their functioning (Grace, 1997).

5.4.5 Functional balance

The functional balance concept assumes that the allocation of assimilates is in a state of equilibrium between the different growing organs in a plant. An example of this is the assumption of functional balance between shoot and root growth in a tree (Mäkelä, 1997). The roots depend on photosynthates that the shoots produce and the shoots require water and nutrients from the roots. To allocate assimilates in an optimal way in the long term, it is assumed that a state of equilibrium must exists between these two components (Sievänen et al., 2000).

5.4.6 Allocation of photosynthates in LIGNUM

The LIGNUM model is one of the first FSTMs published that tries to model the interaction between the functioning and the structural development of a tree using a model in which the tree crown has a detailed and realistic three-dimensional description. The modelling units corresponding to the organs of a tree can sense their local light environment, and the metabolic processes are associated with the units in which they are taking place.

The main contribution of the LIGNUM model is the novel way in which the photosynthates can be allocated among possibly thousands of units (tree segments and buds), each taking its own self- centred but fair share of the available resources.

In the LIGNUM model the general framework for evaluating the growth increment in annual (Perttunen et al. 1998, [III], Perttunen et al. 2001, [IV]) or shorter (Lu, 2006) time steps is to first sum the photosynthates, P, and the respiration losses, M, for the whole tree and then allocate the net production to the growth, G, in different parts of the tree. New growth is possible if the photosynthetic production exceeds the respiration requirements:

$$P - M = G \quad \text{and} \quad P - M > 0 \tag{21}$$

So far there has been no storage module for photosynthates in LIGNUM. If $P - M \leq 0$, then the tree is considered dead and simulation of the tree growth will be stopped.

Carbon balance equation The growth is either primary (elongation) or secondary (diameter growth). The tree creates new tree segments and buds (ΔW_n). The new tree segments induce thickening of the existing segments, (ΔW_o) and the formation of new foliage requires the tree to add new roots(ΔW_r):

$$G = \Delta W_n + \Delta W_o + \Delta W_r \tag{22}$$

The number of new segments is determined by the conditions of the mother tree segments. According to the pipe model, the sapwood in the new segments at the tip of the branches must be matched by the segments below all the way down to the base of the tree and the new foliage requires new roots. The total requirement of photosynthates caused by the new segments cannot be known at the time of their creation. This can only be evaluated by travelling down the tree from the tip of the branches to the stem base and assessing the induced radial growth at each branching point.

Thus, given certain sizes of the new segments, there is no guarantee that Eq. 22 will hold. The balancing or root finding of Eq. 22 must be done iteratively. To do this, let us introduce a unitless parameter λ that affects the lengths of the new segments. That is, when $\lambda = 0$ the lengths of all new segments are equal to 0. When the value of λ increases the new segments become longer (and thicker), and when the value of λ decreases the new segments become shorter (and thinner). Thus, Eq. 22 for growth and photosynthate balance depends on λ:

$$G(\lambda) = \Delta W_n(\lambda) + \Delta W_o(\lambda) + \Delta W_r(\lambda) \tag{23}$$

To solve Eq. 23 at each time step, for example Bisection or van Wijngaarden Dekker-Brent (Press et al., 2002) methods are used in LIGNUM (Perttunen et al. 2001, [IV], Lu 2006).

Extension growth For the extension growth conifers, the number of new buds forking off at the apex of a mother tree segment is modelled as a function of its foliage mass. For deciduous trees (Perttunen et al. 2001, [IV], Lu 2006), the arrangement of the buds along the stem and in the branches follows the observable repeating patterns of the species.

The length, L, of a new segment is determined by one or more of the following multiplicative functions

$$L = \lambda f_1(i_p) f_2(\omega) f_3(\nu) f_4(\psi) \tag{24}$$

where f_1 determines the local light climate, f_2 accounts for the branching, f_3 is the growth potential as a function of the vigour index (Nikinmaa et al., 2000), and f_4 describes the apical dominance. Each of these functions, f_i, have the range [0:1], i.e. each segment receives a fair proportion of the available assimilates. In addition, λ is the parameter for the carbon balance adjustment (Eq. 23).

Diameter growth: pipe model The secondary wood thickening in the LIGNUM model is based on the pipe model hypothesis (Shinozaki et al., 1964). It is assumed that the foliage biomass is associated with a certain cross-sectional area of sapwood below that foliage. Also, the original pipe model idea is modified to allow for the dynamics of the active pipes that the dying foliage releases for reuse. In other words, the dying foliage releases transport capacity in the tree, and the need to transport assimilates to create new sapwood in the branches and in the stem decreases (Nikinmaa, 1992).

New tree segments at the tip of the branches add sapwood cross-sectional area at the distal parts of the of the tree that must be matched by the segment below. The cross-sectional area of sapwood in a tree segment immediately below a branching point must be equal to the sum of the sapwood cross-sectional areas of the segments passing upwards from that branching point. This pipe model requirement must hold at each branching point (i.e. it is invariant).

Two other factors affect radial growth in a segment. First, part of the sapwood dies and turns into heartwood. New sapwood is needed for radial growth in order to compensate for this loss. Second, when the foliage dies in a segment, the corresponding amount of sapwood is released to match the pipe model requirement of the segments above. For coniferous trees (e.g. Perttunen et al. 1996, [I], for Scots pine), the sapwood requirement, $A_{\mathrm{sr}}^{\mathrm{Cf}}$, can be defined in terms of the original sapwood area, A_{s0}:

$$A_{\mathrm{sr}}^{\mathrm{Cf}} = p_f A_{\mathrm{s0}} \tag{25}$$

where p_f is the proportion of initial foliage left. For deciduous species one can assume that a specific unit cross-sectional area of sapwood can support a certain mass of leaves (e.g. Perttunen et al. 2001, [IV], for sugar maple), defined by the empirical parameter, Y. The sapwood or pipe model requirement, $A_{\mathrm{sr}}^{\mathrm{Hw}}$, in a segment for deciduous trees is then:

$$A_{\mathrm{sr}}^{\mathrm{Hw}} = \frac{A_f}{\mathrm{SLA}Y} \tag{26}$$

where A_f is the leaf area in the segment and SLA is the specific leaf area that describes the allocation of leaf biomass per unit of leaf area, also known as a measure of leaf thickness[6].

Denote the senescence of sapwood by dA_s, i.e. that part of the living sapwood which becomes dead heartwood. Assume that the sum of the cross-sectional areas of sapwood in the segments above, A_{su}, is known. Then the new wood area, A_w^{new}, including heartwood and sapwood of the segment, is:

$$A_w^{\mathrm{new}} = \max[A_{\mathrm{su}} + dA_s + A_h + A_{\mathrm{sr}}, A_w] \tag{27}$$

where A_h is the existing heartwood and A_{sr} is the sapwood requirement by the existing foliage (if present) either from Eq. 25 or 26. By choosing the maximum value of the existing wood area, A_w, and the induced diameter growth, Eq. 27 prevents the segment becoming smaller in size. When $A_{\mathrm{sr}} = 0$ the radial growth is defined by the senescence of sapwood and the growth above that point. Eq. 27 prevents the reduction of the segment diameter in case the sapwood area demand from above has decreased strongly.

Eq. 27 implements so-called autonomous sapwood senescence, i.e. part of the sapwood in a tree segment dies each year. This approximates the case where sapwood rings have reached their maximum age. In the foliage-related sapwood senescence, it is assumed that the death of foliage controls the senescence of sapwood. See Section 6.3.

[6]It can be easily shown that the leaf thickness, T, can be expressed as $T = \frac{1}{\rho \mathrm{SLALDMC}}$, where ρ is leaf density and LDMC the leaf dry matter content

6 Three case analyses with LIGNUM

The development of the LIGNUM model has taken place in applications where the model behaviour has been analyzed from the point of view of the application. Sections 6.1 - 6.3 present three such examples. Section 6.1 demonstrates with a Scots pine sapling the importance of the interaction between tree architecture, functioning of the tree and the environment in the context of L systems. Section 6.2 illustrates how different light climates affect the understorey growth of a sugar maple sapling. Section 6.3 serves as an example of how the internal distribution of resources (sapwood senescence) affects Scots pine sapling growth.

6.1 Modelling the interaction between Scots pine functioning and structure.

The study by Perttunen and Sievänen (2005, [V]) presented a formal way to model the architectural development of trees using L systems with the L language (Prusinkiewicz et al., 1999) in the LIGNUM model. The L language has been integrated with LIGNUM so that the strings of L can be translated to structural units of LIGNUM and the results of the physiological activities in LIGNUM can be transferred to the L string.

As an example, Fig. 5 presents three simulations incorporating the work with the Scots pine model (Perttunen et al., 1996, [I], Perttunen et al., 1998, [III]). The L system is presented in Appendix B and the resulting tree architecture after eight derivations without functioning part of LIGNUM is given in Fig. 5(a). The simulations in Figs 5(b) and 5(c) use the same L system to define the architectural development but they model young Scots pine development in two different light climates. The Scots pine in Fig. 5(b) is an open grown sapling. For the Scots pine in Fig. 5(c) half of the model sky was masked from the zenith to the horizon thereby providing no incoming radiation.

The calculations in LIGNUM include the computation of self shading of the tree crown in order to determine the interception of solar radiation and the iterative allocation of net photosynthates to growth. Although in the simulations in Figs 5(b) and 5(c) it is the parameter l in the L system symbol for bud $B(g, l)$ that initially determines the length of a segment (Appendix B), the results of metabolic processes eventually resolve the segment dimensions.

The three simulations with Scots pine demonstrate how LIGNUM can capture the environmental impact (different light regimes) on tree development; the interaction of the L language programme and the functioning part of LIGNUM clearly have a noticeable impact on the outcome of the simulation. The amount and the quality of solar radiation (PAR) have a striking effect on the architecture of the tree. The tree grown with half of the hemisphere shut-off has lost its shaded branches from the right side. Plants are not closed systems but interaction with their environment has an important function in their development.

(a) Tree architecture development by L system only.

(b) Open grown pine. Tree height 4.0m.

(c) Pine in shade, half of the hemisphere masked. Tree height 2.5m.

Figure 5: Three pines all having the same L system as in Appendix B after eight development steps, illustrating the effect of two different light climates.

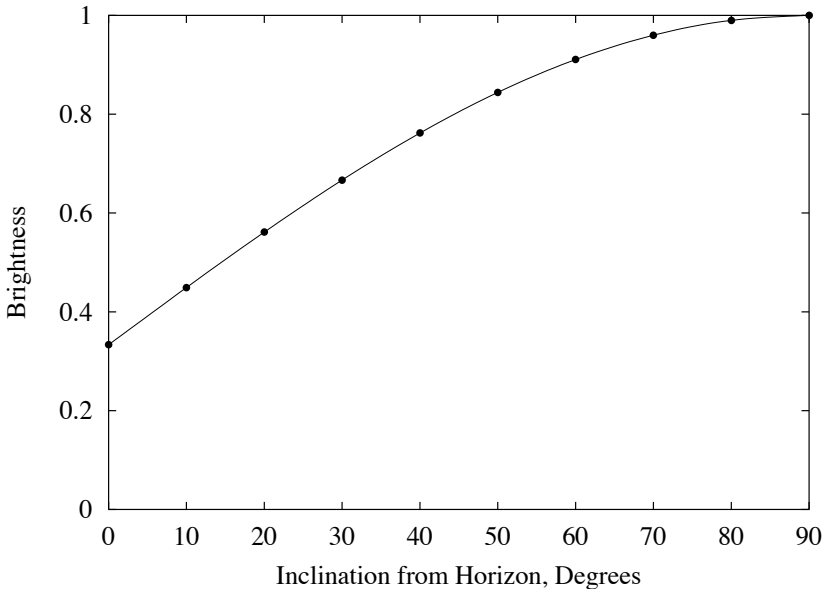
6.2 Modelling the growth of sugar maple saplings in forest gaps

6.2.1 Radiation distribution in forest gaps

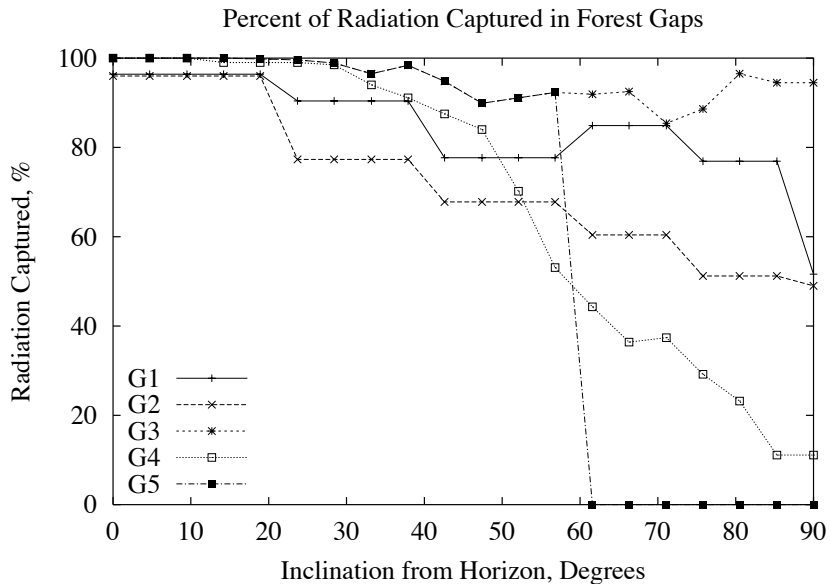
LIGNUM uses the amount of incoming photosynthetically active radiation (PAR) during the growing period as the critical environmental input. Since the real distribution of sky irradiance is not available for PAR the standard overcast sky (SOC Ross, 1981) is applied. In this case sky radiance depends on the inclination (Fig. 6(a)).

The model sky in LIGNUM divides the hemisphere into discrete sectors of equal size. The number of sectors need not be the same for all applications but can be defined according to the requirements of the model. If the SOC model is used then the total unshaded incoming radiant energy of PAR is distributed into the sectors such that that any two sectors with equal inclination have the same brightness. However, the brightness of each sector can be defined individually if needed.

For example, in order to model sugar maple saplings growing in understorey forest gaps (see also Section 6.2.2 Perttunen et al., 2001, [IV]) the open sky radiation of about $1450 MJm^{-2}$ near Abitibi in Quebec, Canada needed to be transformed. Radiation was assessed in selected forest gaps at two locations, Mont St. Hilaire and Duchesney, using hemispheric ('fish eye') photographs. Each photograph gave a template that could be superimposed on the open sky radiation field in order to calculate the attenuation of the radiation and to estimate the distribution of incoming radiation in the gap.



(a) SOC: as the sky radiance depends on inclination, the zenith is about three times brighter than the horizon.



(b) Percentage of radiation captured by the surrounding trees as a function of the inclination measured in forest gaps G1–G5 (100 = no light, 0 = full light). For details about gaps G1–G5, see Section 6.2.1

Figure 6: The relative sky brightness of the SOC 6(a) and the impact of five gap models constructed to simulate the radiation conditions in forest gaps 6(b).

Two gap models (G1 and G2) were constructed for Mont St. Hilaire and three (G3, G4 and G5) for Duchesnay. The fraction of incoming radiation varied from 5.6% to 26.6%. The G5 gap is not real. It was constructed from G3 such that the total amount of radiation is about the same as in G2 and G4 but comes only from directly overhead (Fig. 6(b)).

6.2.2 Sapling growth in forest gaps

The LIGNUM model was applied for sugar maple in order to study sugar maple sapling survival in understorey forest gaps (Perttunen et al., 2001, [IV]). The objective was to produce realistic saplings that matched the observations and measurements made in the field experiments. The physiological parameters required for the sugar maple model were obtained mainly from the literature. Saplings were simulated up to 10 years of age (Fig. 7).

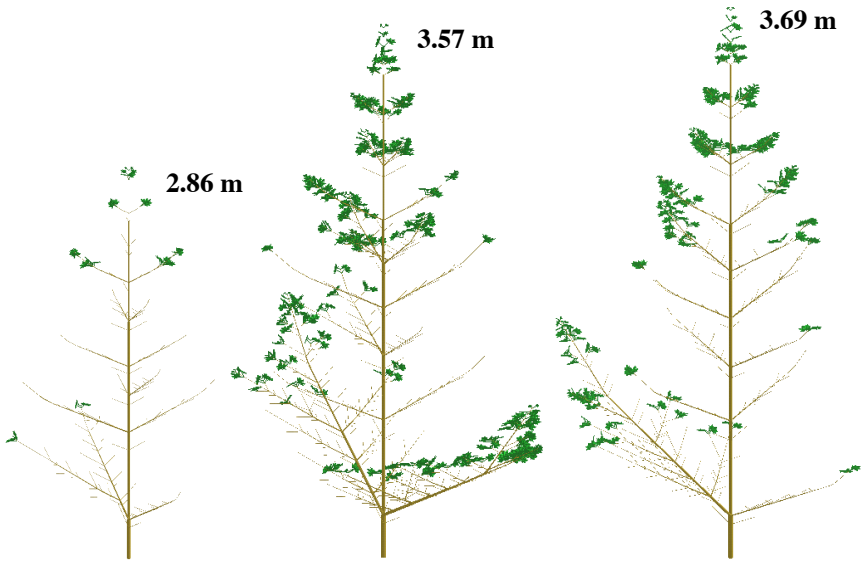
The five gap models G1– G5 are explained in detail in Section 6.2.1. The saplings produced in open gap conditions, G2 and G4 in Fig. 7(a), are similar in appearance. G2 seems to be slightly more vigorous due to the somewhat better radiation conditions but no significant differences in growth can be observed. The simulation in G1 in Fig. 7(a) represents a sapling growing in a closed gap and shows less growth than G2 and G4 due to decreased radiation. The fourth simulation in gap G3 in Fig. 7(b) models relatively low light conditions.

The fifth simulation in gap G5 in Fig. 7(b) demonstrates how FSTMs can be used to consider 'what if' scenarios. The gap opening in G5 has produced a considerably different sapling than in G2 and G4. There is only a small difference in height growth, but the sapling is much bushier due to the PAR available from overhead. Thus, the simulation suggests that not only the amount of PAR but also its directional distribution affects the growth of sugar maple saplings.

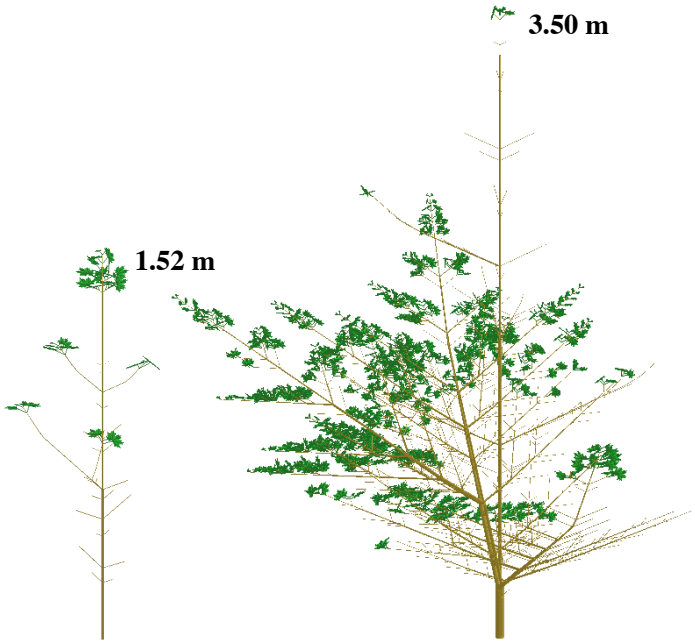
One of the points that make FSTMs attractive in studies regarding, for example, sapling behaviour in scenarios involving gap regeneration is that, in principle, these models are capable of capturing slight differences in resource allocation to structural growth and the feedback for future sapling performance. It may be more important to consider differences in resource allocation than production differences alone when determining the outcome of sapling survival. For details of the study, see Perttunen et al. (2001, [IV]).

6.3 Heartwood formation in Scots pine

Despite the importance of sapwood senescence in tree growth, the actual mechanism that turns sapwood into heartwood is not well known (Mäkelä and Vanninen, 2001). Detailed physiological studies are needed to find the mechanisms involved in heartwood formation. However, FSTMs provide possibilities to study how the senescence of sapwood affects thickness growth to and analyze the implications for tree growth in general in a modelling framework in which tree level behaviour results from the functioning of its parts.



(a) Left: Mont St Hilaire G1. Middle: Mont St. Hilaire G2. Right: Duchesnay G4.



(b) Left: Duchesnay G3. Right: Duchesnay G5

Figure 7: The effect of different light conditions in five forest gaps, G1–G5, on sugar maple sapling development. The five saplings are 10 years old.

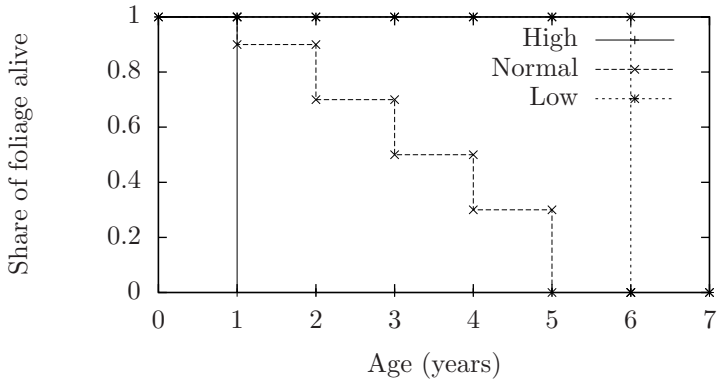


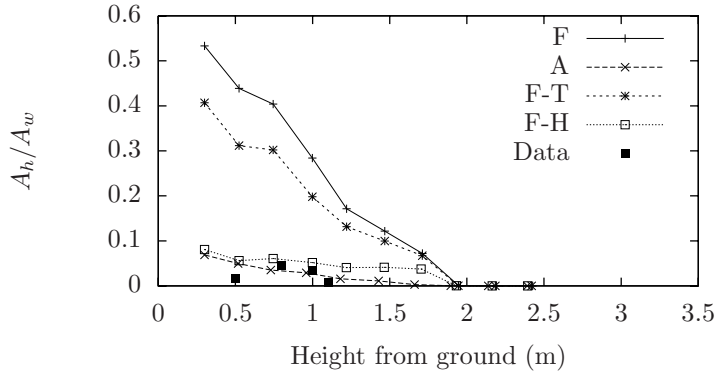
Figure 8: With the high foliage senescence model all the foliage dies after 1 year, in the normal senescence model the foliage gradually dies during a 5-year period, and in the low foliage senescence model all the foliage is retained for 6 years.

Sievänen et al. (1997, [II]) formulated and studied the effect of two rationales, autonomous and foliage-related sapwood senescence, on tree growth with LIGNUM in the context of high, normal and low foliage senescence (Figs. 8 and 9). In the autonomous sapwood senescence (A), part of the sapwood dies annually. In this approach the new wood area for each segment is as in Eq. 27, and diameter of a segment increases if the existing wood area, A_w, increases from the previous year.

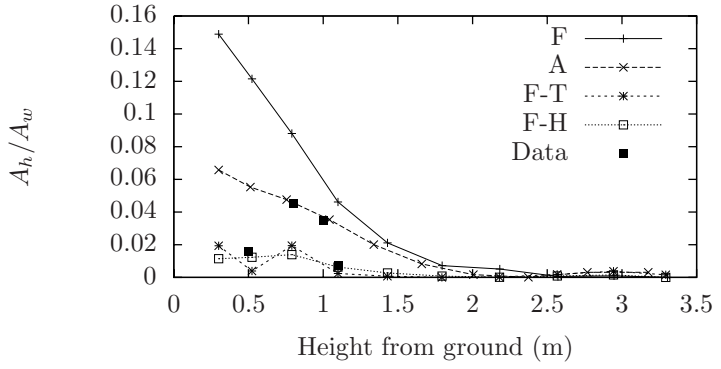
In the foliage related sapwood senescence (F), it is assumed that the death of foliage controls heartwood formation. In this case it is assumed that excess sapwood dies. Excess sapwood exists if the segment has larger sapwood area than matching above sapwood area and own foliage requires. It is also assumed, in accordance with the pipe model, that when a certain area of sapwood dies, the same area of sapwood in segments along the path down to the base of the tree also dies (see Eqs. 7 and 9 in Sievänen et al. (1997, [II])).

Two modifications to foliage related mortality were tested as well. In the first, F-H, half of the formed heartwood area was passed down (Eq. 12 in Sievänen et al. (1997, [II])). In the second case, F-T, a threshold value, p, was applied. Heartwood exceeding a certain share of the sapwood area was passed down (Eq. 13 in Sievänen et al. (1997, [II])).

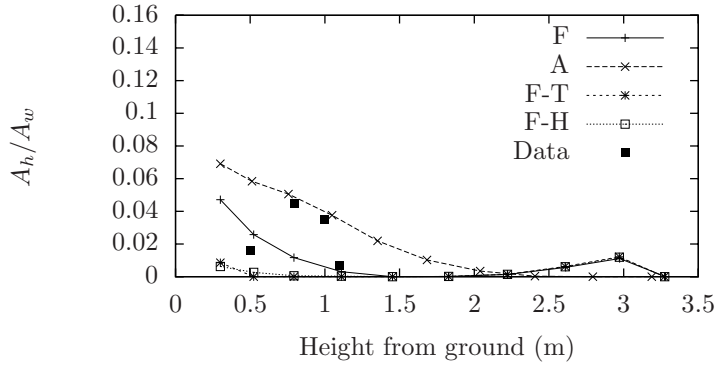
Clearly, the foliage-related sapwood senescence produces more heartwood than the autonomous sapwood senescence model even though no decisive conclusions could be made between the sapwood senescence models. Both of them, with appropriate modifications and parameterization, are able to describe heartwood formation equally well. Thus, the simpler autonomous model appears more attractive on the basis of the limited data available (Fig. 9).



(a) High foliage senescence



(b) Normal foliage senescence



(c) Low foliage senescence

Figure 9: Simulated proportion of heartwood (A_h/A_w) for high, normal and low foliage senescence models. A_h = heartwood area and A_w = cross sectional area of the segment. Sapwood senescence: F = foliage related, A = autonomous, F-H = foliage related, half of the formed sapwood is passed down, F-T = foliage related, threshold value $p = 0.05$. Superimposed on the three panels are mean heartwood proportions of the data from Lukkarinen (1992) at distances 2.2, 2.3, 2.5 and 2.8 m from the tree top.

7 Conclusions

The LIGNUM functional-structural tree model integrates both the functional and structural aspects of woody arborescent plants in a single modelling framework. One of the novelties of the model is its allocation of photosynthates while taking into consideration feedback from the new tree structure in the future production of the tree based on the interaction with the (light) environment using a detailed three-dimensional representation of the tree crown consisting of possibly thousands of functioning units.

The LIGNUM model has been applied to both coniferous (Perttunen et al., 1996, [I], Lo et al., 2001) and deciduous species (Perttunen et al., 2001, [IV], Sievänen et al., 2004, Lu, 2006) and clonal dwarf shrubs (Salemaa et al., 2006). The work of Lu (2006) on fast-growing cottonwood includes the implementation of short time step with the photosynthesis model of Farquhar et al. (1980). Also, LIGNUM has been used in the pursuit of modelling (with simplified assumptions) small forests plots (Perttunen et al., 2004; Lu, 2006; Perttunen et al., 2007). The model structure of LIGNUM is adaptable for the parameterization of new species and provides a well-founded modelling framework for trees or woody perennial plants in general.

Apart from applying LIGNUM to different tree species, other applications have been realised on the basis of LIGNUM's representation of a tree. It has been adapted as a tool to study tree decay (Heikura, 2007). Based on the sudy material, the application generates three-dimensional models of urban trees and can be used to analyse their wounds, cracks and cavities (Terho et al., 2007). It has been used to reconstruct the three-dimensional crown structure of Scots pine crowns on the basis of digitized measurements (Kaitaniemi et al., 2007). It has been integrated into the interactive software tool PuMe (Vanninen et al., 2006) for forestry studies at secondary level schools and in universities in Finland. The PipeQual growth simulator (Mäkelä, 2003) in PuMe produces traditional characteristics about the simulated trees, such as stem shape, location of branches, heartwood, sapwood etc. and LIGNUM is used to generate detailed three-dimensional models of these trees in order to illustrate their structural differentiation. Three-dimensional tree crowns generated with the aid of structural measurements have been employed in electromagnetic scattering studies of a forest in a remote sensing application (Praks et al., 2003).

The carbon allocation and reserve dynamics are features that can be improved in the LIGNUM model. Currently, all net photosynthates are allocated to structure for carbon assimilation (foliage), growth (stem and branches) and support of the tree (roots). But the function of reserve dynamics should not be trivialised or neglected. The reserves are means which the trees use to prepare and cope with threats and are important in the adaptation to particular environments. Although the process is poorly known, for example the saplings of shade-tolerant deciduous understorey species (e.g. sugar maple) flush their leaves a few weeks earlier than the overstorey species (e.g. aspen, birch). This short period gives the understorey plants the opportunity for a high growth rate and allocation to storage. The allocation of storage might be important because the rest of the growing period will be characterized by low light conditions, followed by winter

dormancy. Thus, early leaf flush and allocation to storage might be the strategy which shade tolerant species utilize to adapt to survive, and then take the place of early successional tree species. (Walters and Reich, 1999).

The root system is described with one variable in LIGNUM. However, very few FSTM models take into account below-ground processes, and even then only with s relatively coarse model for water and nutrient uptake and allocation (Le Roux et al., 2001). Trees are not only made of carbon but nitrogen, and other nutrients are important for biological processes, for example, photosynthesis and respiration. Thus, for many applications it is worth modelling not only the structure and functioning of the root system but also the uptake, development and allocation of nutrient supply.

Bud fate is especially important for deciduous species, i.e. whether the bud becomes active and grows to create new structure, remains dormant or dies. The implementation of bud activity for deciduous trees in LIGNUM (Perttunen et al., 2001, [IV]) is so far only simplified, but the question is also a research problem in tree physiology and requires a more fundamental experimental approach than has been used so far.

FSTMs show potential as a tool to include and analyze the effects of genetic variation in trees. If the parameter values of the model are based on genetic information, this could provide a new understanding of plant development and open up possibilities to study and analyze, for example, the effects of environment on different genotypes (Prusinkiewicz, 2004; Buck-Sorlin et al., 2005; Prusinkiewicz et al., 2007a).

To scale up from single trees to modelling the development of forest plots is an idea that arises inherently but requires careful assessment in FSTM. One possibility to create a forest canopy is to use duplicates of an individual tree (Perttunen et al., 2007) or use slightly different trees. However, it is unclear whether the canopies constructed in this manner behave like real canopies. Some of the heterogeneity of the canopy can be achieved to describe, for example, the radiation regime but the idiosyncrasy is that the tree is competing with itself. It is a tempting thought to simulate a small forest plot consisting of individual trees that realistically model the emergent competition between plants. In practice, however, this may require the use of parallel computers.

Finally, modellers should work jointly with experimental scientists so that the FSTMs are based on well-founded knowledge of tree physiology. The feedback between experimental studies based on different points of view and the modelling work can integrate knowledge and provide new insights into tree and plant life that cannot be achieved if the morphological and physiological aspects of tree functioning are studied separately.

References

Abelson, H., di Sesa, A. A., 1982. Turtle geometry. M.I.T Press, Cambridge.

Allen, M., Prusinkiewicz, P., DeJong, T., 2005. Using l-systems for modeling source-sink interactions, architecture and physiology of growing trees: the L-PEACH model. New Phytologist 166 (3), 869–880.

Allen, M., Prusinkiewicz, P., Favreau, R., DeJong, T., 2007. L-PEACH, an L-system-based model for simulating architecture, carbohydrate source-sink interactions and physiological responses of growing trees. In: Vos, J., L.F.M., M., de Visser, P., Struik, P., Evers, J. (Eds.), Functional-Structural Plant Modelling in Crop Production. Vol. 22 of Wageningen UR Frontis Series. Springer, Netherlands, pp. 139–150.

Ancelin, P., Fourcaud, T., Lac, P., 2004. Modelling the biomechanical behaviour of growing trees at the forest stand scale. part i: Development of an incremental transfer matrix method and an application to simplified tree structures. Ann. For. Sci 2004, 263–275.

Balandier, P., Lacointe, A., Le Roux, X., Sinoquet, H., 2000. Simwal: a structure-function model simulating single walnut tree growth according to climate and pruning. Ann. For. Sci 57, 571–585.

Barthélémy, D., Caraglio, Y., 2007. Plant architecture: A dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. Annals of Botany 99, 375–407.

Bell, A., 1991. Plant form, an illustrated guide to flowering plant morphology. Oxford University Press, Oxford.

Blaise, F., Barczi, J., Jaeger, P., Dinouard, P., de Reffye, P., 1998. Simulation of the growth of plants - modeling of metamorphosis ans spatial interaction in the architecture and development of plants. In: Cyberworlds. Springer, Tokyo, pp. 81–109.

Bossel, H., 1996. Treedyn3 forest simulation model. Ecological Modelling 90 (2), 187–227.

Boudon, F., Meyer, A., Godin, C., 2006. Survey on computer representations of trees for realistic and efficient rendering. Research report 2301, LIRIS, Université Claude Bernard Lyon 1.

Boudon, F., Prusinkiewicz, Przemyslaw, P., Federl, P., Godin, C., Karwowski, R., 2003. Interactive design of bonsai tree models. In: Proceedings of Eurographics 2003: Computer Graphics Forum 22 (3). pp. 591–599.

Brisson, J., 2001. Neighborhood competition and crown assymmetry in *Acer saccharum*. Can. J. For. Res. 31, 2151–2159.

Buck-Sorlin, G., Kniemeyer, O., Kurth, W., 2005. Barley morphology, genetics and hormonal regulation of internode elongation modelled by a relational growth grammar. New Phytologist 166 (3), 859–867.

Cescatti, A., 1997. Modellling the radiative transfer in discontinuous canopies of asymmetric crowns. i. model structure and algorithms. Ecol. Modell. 101, 263–274.

Cheeseman, J., Lexa, M., 1996. Gas exchange: models and measurements. In: Baker, N. (Ed.), Photosynthesis and Environment. Vol. 5 of Advances in Photosynthesis. Kluwer Academic Publishers, Dordrecht, pp. 281–300.

Chelle, M., Andrieu, B., 2007. Modelling the light environment of virtual crop canopies. In: Vos, J., L.F.M., M., de Visser, P., Struik, P., Evers, J. (Eds.), Functional-Structural Plant Modelling in Crop Production. Vol. 22 of Wageningen UR Frontis Series. Springer, Netherlands, pp. 75–89.

Cournède, P.-H., Mathieu, A., Houllier, F., Barthélémy, de Reffye, P., 2007. Computing competition for light in the GREENLAB model plant growth: A contribution to the study of the effects of density on resource acquisition and architecural development. Annals of Botany, 1–13.

de Reffye, P., Cournède, P., 2005. A powerful factorisation method to compute plant architecture, applications in agronomy and computer graphics. In: 1st Open International Conference on Modeling and Simulation (OICMS), June 12–15, 2005, ISIMA/Blaise Pascal University. ISIMA/Blaise Pascal University, pp. 13–26.

de Reffye, P., Dinouard, P., Guédon, Barthélémy, D., 1991. Modélisation et simulation de l'architecture et de l'orme du japon textitZelkova serrata (thunb.) makino *(Ulmaceae)*: la notion d'axe de référence. In: Edelin, C. (Ed.), Naturalia Monspeliensia, N hors série A7. Montpellier, France, pp. 251–266.

de Reffye, P., Fourcaud, T., Blaise, F., Barthélémy, D., Houllier, F., 1997. A functional model of tree growth and tree architecture. Silva Fennica 31 (3), 297–311.

de Reffye, P., Houllier, F., 1997. Modelling plant growth and architecture: Some recent advances and applications to agronomy and forestry. Current Science 73 (11), 984–992.

de Reffye, P., Houllier, F., Blaise, F., Barthélémy, D., Dauzat, J., Auclair, D., 1995. A model simulating above and below ground tree architecture with agroforestry applications. Agroforestry Systems 30, 175–197.

de Reffye, P., Hu, B.-G., 2003. Relevant qualitative and quantitative choises for building an efficient dynamic plant growth model: Greenlab case. In: Hu, B.-G., Jaeger, M. (Eds.), Plant Growth Modeling and Applications Proceedings - PMA03, 2003 International Symposium on Plant Growth Modeling, Simulation, Visualization and their Applications, Bejing, China, October 13–16, 2003. Tsinghua University Press, Springer, pp. 87–107.

Deleuze, C., Houllier, F., 1995. Prediction of stem profile of *Picea abies* using a process-based tree gorwth model. Tree Phyiol. 15, 113–120.

Dzierzon, H., 2003. Development of methods for characterizing plant and stand architectures and for model competition. Ph.D. thesis, Fakultät für Forstwissenschaften und Waldökologie der Georg-August-Universität Göttingen.

Dzierzon, H., Kurth, W., 2002. Lignum: a finnish tree growth model and its interface to the french amapmod database. In: Hölker, F. (Ed.), Scales, Hierarchies and Emergent Properties in Ecological Models. Peter Lang, Frankfurt a. M., p. 95104.

Dzierzon, H., Perttunen, J., Kurth, W., Sievänen, R., Sloboda, B., 2003. Enhanced possibilities for analyzing tree structure as provided by an interface between different modelling systems. Silva Fennica 37 (1), 31–44.

Farquhar, G., von Caemmerer, S., Berry, J., 1980. A biochemical model of photosynthesic CO_2 assimilation in leaves of C_3 plants. Planta 149, 78–90.

Ferraro, P., Godin, C., Prusinkiewicz, P., 2002. L-systems and MTGs: Integrating simulation and formal analysis of architectural plant models. In: Krzysztof, A., Meuth, H. (Eds.), 16th European Simulation Multiconference. Modelling and Simulation 2002. SCS Europe, Erlangen, Germany, pp. 418–422, ESM 2002, 3–5 June 2002, Darmstadt, Germany.

Fisher, J. B., Honda, H., 1977. Computer simulation of branching pattern and geometry in terminalia (combretaceace), a tropical tree. Bot. Gaz. 138 (4), 377–384.

Fourcaud, T., Lac, P., 1996. Mechanical analysis of the form and internal stresses of a growing tree by the finite element method. In: Engin, A. (Ed.), Engineering Systems Design Analysis Proceedings, ASME. Vol. 77. pp. 213–220.

Godin, C., 2000. Representing and encoding plant architecture: A review. Ann. For. Sci. 57, 413–438.

Godin, C., Caraglio, Y., 1998. A multiscale model for plant topological structures. Journal of Theoretical Biology 191, 1–46.

Godin, C., Costes, E., Sinoquet, H., 1999. A method for describing plant architecture wich integrates topology and geometry. Annals of Botany 84 (3), 343–357.

Godin, C., Guédon, Y., Costes, E., Caraglio, Y., 1997. Measuring and analyzing plants with the amapmod software. In: Michalewicz, M. (Ed.), Plants to ecosystems - Advances in Computational Life Sciences 2nd International Symposium on Computer Challenges in Life Science. CSIRO Publishing, Australia, pp. 53–84.

Grace, J., 1997. Plant water relations. In: Crawley, M. (Ed.), Plant Ecology. Blackwell Science, Cambridge, pp. 28–50.

Gravelius, H., 1914. Flusskunde. Goschen, Berlin.

Grossmann, Y., DeJong, T., 1994. PEACH: A simulation model of reproductive and vegetative growth in peach trees. Tree Physiol. 14, 329–345.

Hallé, F., Oldeman, R., 1970. Essai surl'architecture et la dynamique de croissance des arbres tropicaux. Masson et Cie, Paris.

Hallé, F., Oldeman, R. A. A., Tomlinson, P. B., 1978. Tropical trees and forests. Springer Verlag, Berlin.

Hanan, J., Prusinkiewicz, P., Zalucki, M., Skirvin, D., 2002. Simulation of insect movement with respect to plant architecture and morphogenesis. Computers and Electroincs in Agriculture 35, 255–269.

Hari, P., E., N., Holmberg, M., 1990. Photosynthesis, transpiration and nutrient upake in relation to tree structure. In: Dixon, R., Meldahl, R., G.A., R., Warren, W. (Eds.), Process modelling of forest growth responses to environmental stress. Timber Press, Portland, Oregon, Ch. 4, pp. 50–57.

Hari, P., Kellomäki, S., Mäkelä, A., Ilonen, P., Kanninen, M., Korpilahti, E., Nygren, M., 1982. Dynamics of early development of tree stand. Acta Forestalia Fennica 177.

Hearn, D., Baker, M. P., 1994. Computer Graphics, 2nd Edition. Prentice Hall, Englewood Cliffs, New Jersey, Ch. 14-6, p. 362.

Heikura, T., November 2007. Puiden lahovaurioiden analysointi kolmiulotteisen rakennemallin ja kuvamittauksen avulla. *Ananlysis of tree decay using photogrammetry and a three dimensional structural model*. Master's thesis, Helsinki University of Technology.

Honda, H., 1971. Description of the form of trees by the parameters of the tree-like body: effects of the branching angle and branching length on the shape of the tree-like body. J. Theor. Biol. 31, 331–338.

Host, G., Rauscher, H., Isebrands, J., Michael, D., 1990. Validation pof photsynthate production of ECOPHYS, an ecophysiological growth prcess model of *Populus*. Tree Physiol. 7, 283–296.

Kaitaniemi, P., Perttunen, J., Sievänen, R., 2007. Digitizing as a tool for modeling the 3D architecture of tree crowns. In: International Conference on Wind and Trees, IUFRO 8.0.11, August 5-9, 2007, Vancouver, British Columbia, Canada.

Karwowski, R., October 2002. Improving the process of plant modeling: The L+C modeling language. Ph.D. thesis, University of Calgary.

Karwowski, R., Prusinkiewicz, P., 2003. Design and implementation of the L+C modelling language. Electronic Notes in Theoretical Computer Science 86 (2), Accepted.

Kellomäki, S., Strandman, H., 1995. A model for structural growth of young scots pine crowns based on light interception by shoots. Ecological Modelling 80, 237–250.

Kniemeyer, O., Buck-Sorlin, G., Kurth, W., 2007. GroIMP as a platform for functional-structural modelling of plants. In: Vos, J., Marcelis, L., de Visser, P., Struik, P., Evers, J. (Eds.), Functional-Structural Plant Modelling in Crop Production. Springer, Printed in the Netherlands, pp. 43–52.

Knyazikhin, Y., Marshak, A., Myneni, R., 1998. Influence of small-scale structure on radiative transfer and photosynthesis in vegetation canopies. Journal of Geophysical Research 103, 6133–6144.

Koch, G. W., Sillet, S. C., Jennings, G. M., Davis, S. D., April 2004. The limits to tree height. Nature 428, 851–854.

Kurth, W., 1994. Growth grammar interpreter GROGRA 2.4: A software tool for the 3-dimensional interpretation of stochastic, sensitive growth grammars in the context of plant modeling. Introduction and reference manual. Forschungszentrum Waldökosysteme der Universitet Göttingen, G̈ttingen.

Kurth, W., 1999. Die Simulation der Baumarchitektur mit Wachstumsgrammatiken. Wissenschaftlicher Verlag, Berlin, 327 p.

Kurth, W., 2000. Towards universality of growth grammars: Models of bell, pagès and takenaka revisited. Ann. For. Sci. 57, 543–554.

Kurth, W., Kniemeyer, O., Buck-Sorlin, G., 2005. Relational growth grammars – a graph rewriting approach to dynamical systems with dynamical structure. In: Banâtre, J.-P., Fradet, P., Giavitto, J.-L., Michel, O. (Eds.), Unconventional Programming Paradigms. International Workshop UPP 2004, Le Mont Saint Michel, France, September 2004. Revised Selected and Invited Papers. Vol. 3566 of Lecture Notes in Computer Science. pp. 56–72.

Kurth, W., Sloboda, B., 2001. Sensitive growth grammars specifying models of forest structure, competition and plant-herbivore interaction. In: Rennols, K. (Ed.), Proceedings of the IUFRO 4.11 Congress "Forest Biometry, Modelling and Information Science, Greenwich, UK (25-29.6.2001. pp. 1–15.

Lacointe, A., 2000. Carbon allocation among tree organs: A review of basic processes and representation in functional-structural models. Ann. For. Sci. 57, 521–533.

Landsberg, J., 2003. Physiology in forest models: History and the future. FBMIS 1, 49–63.

Landsberg, J., Gower, S., 1997. Applications of physiological ecology to forest management. Physiological Ecology. Academic Press, San Diego, Ch. 5, pp. 125–160.

Landsberg, J. J., 1986. Physiological Ecology of Forest Production. Academic Press, London.

Le Roux, X., Grand, S., Dreyer, E., Daudet, F., 1999. Parameterization and testing a biochemically based photosynthesis model for walnut (*Junglans regia*) trees and seedlings. Tree Physiology 19, 481–492.

Le Roux, X., Lacointe, A., Escobar-Gutiérrez, A., Dizès, S. L., 2001. Carbon-based models of individual tree growth: A critical appraisal. Ann. For. Sci. 58, 469–506.

Lenz, K. E., Stech, Harlan, W., Host, G. E., 2004. Phenological process models based on carbon productivity at the leaf and branch levels, and their effects on Aspen tree architecture. In: Godin, C., Hanan, J., Kurth, W., Lacointe, A., Takenaka, A., Przemyslaw, P., DeJong, T., Beveridge, C., Andrieu, B. (Eds.), Proceeding of the 4th International Workshop on ' Functional-Structural Plant models. 07-11 June 2004, Campus ENSAM/INRA2, place Viala. Montpellier, France. pp. 120–123.

Lindenmayer, A., 1968. Mathematical models for cellular interaction in development, parts I and II. J. Theor. Biol. 18, 280–315.

Lo, E., Zhang, M. W., Lechowicz, M., Messier, C., Nikinmaa, E., Perttunen, J., 2001. Adaptation of the LIGNUM model for simulations of growth and light response in jack pine. Forest Ecology and Management. 150, 279–291.

Long, S., 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO_2 concentrations: Has its importance been underestimated. Plant, Cell and Environment 14, 729–739.

Lu, M., 2006. Simulating cottonwood tree growth in flood plains using the LIGNUM modelling method. Ph.D. thesis, University of Missouri-Columbia.

Lukkarinen, E., 1992. Männyn pituus- ja paksuuskasvun suhde. Master's thesis, University of Helsinki. Department of Forest Resources.

Mäkelä, A., 1985. Differential games in evolutionary theory: Evolutionary stable height growth strategies of trees. Theoretical Population Biology 27, 239–267.

Mäkelä, A., 1997. Carbon balance model of growth and self-pruning in trees based on structural relationships. Forest Science 43 (1), 7–24.

Mäkelä, A., 2003. Process-based modelling of tree and stand growth: towards a hierarchical treatment of multiscale processes. Can. J. For. Res. 33, 398–409.

Mäkelä, A., Hari, P., 1986. Stand growth model based on carbon uptake and allocation in individual trees. Ecological Modelling 33, 315–331.

Mäkelä, A., Landsberg, J., Ek, A. R., Burk, T. E., Ter-Mikaelian, M., Ågren, G. I., Oliver, C. D., Puttonen, P., 2000. Process-based models for forest ecosystem management: current state of the art and challenges for practical implementation. Tree Physiology 20, 289–298.

Mäkelä, A., Sievänen, R., 1992. Height growth strategies in open-grown trees. Journal of Theoretical Biology 159 (4), 443–467.

Mäkelä, A., Vanninen, P., 2001. Vertical structure of scots pine crowns in different age and size classes. Trees 15, 385–392.

Marcelis, L., Heuvelink, E., 2007. Concepts of modelling carbon allocation among plant parts. In: Vos, J., Marcelis, L., de Visser, P., Struik, P., Evers, J. (Eds.), Functional-Structural Plant Modelling in Crop Production. Springer, Printed in the Netherlands, pp. 43–52.

Marks, C., Lechowicz, M., 2006. A holistic tree seedling model for the investigation of functional trait diversity. EcologicalModelling 193, 141–181.

Matala, J., Hynynen, J., Miina, R., Ojansuu, H., Peltola, R., Sievänen, R., Väisänen, H., Kellomäki, S., 2003. Comparison of a physiological model and a statistical model for prediction of growth and yield in boreal forests. Ecological Modelling 161, 95–116.

McCree, K., 1970. An equation forn the rate of respiration of white clover plants grown under controlled conditions. In: Proceedings of the technical meeting IBP, Trebon (CSK). Centre for Agricultural Publishing and Documentation, Wageningen, (NDL), pp. 221–229.

Mutke, S., Sievänen, R., Nikinmaa, E., Perttunen, J., Gil, L., 2005. Crown architecture of grafted stone pine (*(P)inus pinea* l.): shoot growth and bud differentiation. Trees 19, 15–25.

Nikinmaa, E., 1992. Analysis of the growth of scots pine; matching structure with function (seloste: Analyysi männyn kasvusta; rakenteen sopeutumista aineenvaihduntaan). Acta Forestalia Fennica 235.

Nikinmaa, E., Messier, C., Sievänen, R., Perttunen, J., Lehtonen, M., 2000. Shoot growth and crown development; the effect of crown position in 3D simulations. Tree Physiology.

Oker-Blom, P., Smolander, H., 1988. The ratio of shoot silhouette area to total needle area in scots pine. For. Sci. 34 (4), 894–906.

Perttunen, J., Nikinmaa, E., Lechowicz, M. J., Sievänen, R., Messier, C., 2001. Application of the functional-structural tree model LIGNUM to sugar maple saplings (*Acer saccharum* Marsh) growing in forest gaps. Annals of Botany 88 (3), 471–481.

Perttunen, J., Sievänen, R., 2005. Incoroprating linenmayer systems for architectural development in a functional-structural tree model. Ecological Modelling 181, 479–491.

Perttunen, J., Sievänen, R., Nikinmaa, E., 1998. LIGNUM: A model combining the structure and the functioning of trees. Ecological Modelling 108 (1–3), 189–198.

Perttunen, J., Sievänen, R., Nikinmaa, E., 2007. Assessing the light environment for scots pine in the functional-structural tree model LIGNUM. In: Prusinkiewicz, P., Hanan, J., Lane, B. (Eds.), Proceedings of the 5th International Workshop on Functional-Structural Plant Models. Napier, New Zealand, November 4–9, 2007. pp. 59–1 – 59–5.

Perttunen, J., Sievänen, R., Nikinmaa, E., Lehtonen, M., 2004. On the structural plasticity of Scots pine during early stand development. In: Godin, C., Hanan, J., Kurth, W., Lacointe, A., Takenaka, A., Prusinkiewicz, P., DeJong, T., Beveridge, C., Bruno, A. (Eds.), 4th International Workshop on Functional-Structural Plant Models, 07-11 June 2004. Campus ENSAM/INRA2, place Viala, Montpellier, France, pp. 231–234.

Perttunen, J., Sievänen, R., Nikinmaa, E., Salminen, H., Saarenmaa, H., Väkevä, J., 1996. LIGNUM: A tree model based on simple structural units. Annals of Botany 77 (1), 87–98.

Praks, J., Pulliainen, J., Ahtonen, P., Hallikainen, M., 2003. Examination of forest polarimetric backscattering with coherent cylinder model. In: Geoscience and Remote Sensing Symposium, 2003. IGARSS '03. Proceedings. 2003 IEEE International. Vol. 2. pp. 923–925.

Prentice, I., Sykes, M., Cramer, W., 1993. A simulation model for the transient effects of climate change on forest landscapes. Ecol. Modelling 65, 51–70.

Press, W. H., Teukolsky, S. A., Vetterling, W. T., Flannery, B. B., 2002. Numerical Recipies in C++. The Art of Scientific Computing, 2nd Edition. Cambridge University Press, The Pitt Building, Trunpington Street, Cambridge CB2 1RP, Ch. 9, pp. 267–269.

Prusinkiewicz, P., 1986. Graphical applications of L-systems. Proceedings of Graphics Interface '86 – Vison Interface '86, 247–253.

Prusinkiewicz, P., 1999. A look at the visual modeling of plants using L-systems. Agronomie 19, 211–224.

Prusinkiewicz, P., 2000. Simulation modeling of plants and plant ecosystems. Communations of the ACM 43 (7), 84–93.

Prusinkiewicz, P., 2004. Art and science for life: Designing and growing virtual plants. In: Davidson, C., Fernandez, T. (Eds.), Nursery Crops: Development, Evaluation, Production and Use: Proceedings of the XXVI International Horticultural Congress. Vol. 630 of Acta Horticulturae. pp. 15–28.

Prusinkiewicz, P., Erasmus, Y., Lane, B., Harder, L., Coen, E., 8 June 2007a. Evolution and development of inflorescence architecture. Science 316, 1452–1456.

Prusinkiewicz, P., Hanan, J., Hammel, M., Měch, R., 1997. L-systems: from the theory to the visual models of plants. In: Michalewicz, M. (Ed.), Plants to Ecosystems. Advances in Computational Life Sciences. CSIRO, Collingwood, Australia, pp. 1–27.

Prusinkiewicz, P., Hanan, J., Lane, B. (Eds.), 2007b. Proceedings of the 5th International Workshop on Functional-Structural Plant Models.

Prusinkiewicz, P., Karwowski, R., Lane, B., 2007c. The L+C plant modelling language. In: Vos, J., Marcelis, L., Visser, P., Struik, P., Evers, J. (Eds.), Functional-Structural Plant Modelling in Crop Production. Vol. 22 of Wageningen UR Frontis Series. Springer, Printed in the Netherlands, Ch. 3, pp. 27–42.

Prusinkiewicz, P., Karwowski, R., Perttunen, J., Sievänen, R., 1999. Specification of L – a plant modeling language based on L-systems. version 0.5. Tech. rep., Department of Computer Science, University of Calgary, Internal report.

Prusinkiewicz, P., Lindenmayer, A., 1990. The Algorithmic Beauty of Plants. Springer-Verlag, New York.

Rauscher, H., Isebrands, J., Host, G., Dickson, R., Dickmann, D., Crow, T., Michael, D., 1990. ECOPHYS: And ecophysiological growth process model for poplar. Tree Physiol. 7, 255–281.

Rogers, D. F., Alan, A. J., 1990. Mathematical Elements for Copmuter Graphics, second edition Edition. McGraw-Hill, Singapore, Ch. 6-4, pp. 400–408.

Ross, J., 1981. The Radiation Regime and Architecture of Plant Stands. Dr W. Junk Publishers, Hague, Ch. II.2.3, pp. 161–164.

Salemaa, M., Perttunen, J., Sievänen, R., Tolvanen, A., 2006. Structural development of vaccinium vitis-idaea after rhizome cutting. In: 8th Clonal Plant Workshop. Generality, Specificity, and Diversity of Clonal Growth. June 27–30 2006, Pärnu, Estonia.

Salemaa, M., Sievänen, R., 2002. The effect of apical dominance on the branching architecture of *Arctostaphylos uva-ursi* in four contrasting environments. Flora 197 (1189), 1–14.

Salminen, H., Saarenmaa, H., Perttunen, J., Sievänen, R., Nikinmaa, E., Väkevä, J., 1994. Modelling trees with object oriented scheme. Math. Comput. Model 20 (8), 49–64.

Shinozaki, K., Yoda, K., Hozumi, K., Kira, T., 1964. A quantitive analysis of plant from - the pipe model theory. Jpn. J. Ecol. 14.

Sievänen, R., 1993. A process-based model for the dimensional growth of even-aged stands. Scan J For Res 8 (1), 28–48.

Sievänen, R., Delagrange, S., Messier, C., Nikinmaa, E., Perttunen, J., 2004. Functional structural analysis of understorey seedling peerformance in variable level of shading. In: Godin, C., Hanan, J., Kurth, W., Lacointe, A., Takenaka, A., Przemyslaw, P., DeJong, T., Beveridge, C., Andrieu, B. (Eds.), Proceeding of the 4th International Workshop on ' Functional-Structural Plant models. 07-11 June 2004, Campus ENSAM/INRA2, place Viala. Montpellier, France. p. 329.

Sievänen, R., Nikinmaa, E., Nygren, P., Ozier-Lafontaine, H., Perttunen, J., Hakula, H., 2000. Components of functional-structural tree models. Ann. For. Sci. 57, 399–412.

Sievänen, R., Nikinmaa, E., Perttunen, J., 1997. Evaluation of importance of sapwood senescence on tree growth using the model Lignum. Silva Fennica 31 (3), 329–340.

Sinoquet, H., Roux, X. L., 2000. Short term interactions between tree foliage and the aerial environment: An overview of modelling approaches available for tree structure-function models. Ann. For. Sci. 57, 477–496.

Sorrensen-Cothren, K., Ford, E., Sprugel, D., 1993. A model for competition incorporating plasticity through modular foliage and crown development. Ecological Monograph 63, 227–304.

Sprugel, D., Benecke, U., 1991. Woody-tissue respiration and photosynthesis. In: Lassoie, J., Hinckley, T. (Eds.), Technics and approaches in forest tree ecophyiology. CRC Press, Boca Raton, FL, USA, pp. 329–347.

Sterck, F., Schieving, F., 2007. Growth patterns of tree: effects of carbon economy, meristem activity and selection. Ecological Monographs 77 (3), 405–420.

Sterck, F., Schieving, F., Lemmens, A., Pons, T., 2005. Performance of trees in forest canopies: explorations with a bottom-up functional-structural plant growth model. New Phytologist 166, 827–843.

Stroustrup, B., 1997. The C++ programming language, 3rd Edition. Addison Wesley.

Takenaka, A., 1994. A simulation model of tree archtiecture development based on local light environment. J. Plant Res. 107, 321–330.

Terho, M., Hantula, J., Hallaksela, A.-M., 2007. Occurrence and decay patterns of common wood-decay fungi in hazardous trees felled in the helsinki city. Forest Pathology.

Thomas, P., 2000. Trees: Their Natural History. Cambridge University Press, The Edinburgh Building, Cambridge CB2 2RU, UK.

Thornely, J., 1972. A model to describe the partitioning of photosynthates during vegetative plant growth. Ann. Bot. 36, 431–441.

Thornley, J., 1970. Respiration, growthn and maintenance in plants. Nature 227, 304–305.

Thornley, J. H. M., 1991. A transport-resistance model of forest growth and partitioning. Annals of Botany 68, 211–226.

Tobin, B., Čermák, J., Chiatante, D., Danjon, F., Di Iorio, A., Dupuy, L., Eshel, A., Jourdan, C., Kalliokoski, T., Laiho, R., Nadezhdina, N., Nicoll, B., Pagès, L., Silva, J., Spanos, I., 2007. Towards developmental modelling of tree root systems. Plant Biosystems 141 (3), 481–501.

Tomlinson, P., 1983. Tree architecture. American Scientist 71, 141–149.

Vanninen, P., Härkönen, S., Enkenberg, J., Mäkelä, A., 2006. Pume - interactive learning environment employing the pipequal model for forest growth and wood quality. New Zealeand Journal of Forestry Science 36 (2/3), 280–292.

von Caemmerer, S., 2000. Biochemical Models of Leaf Photosynthesis. No. 2 in Techniques in Plant Sciences. CSIRO Publishing.

von Caemmerer, S., Farquhar, G., 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153, 376–387.

Voss, J., Marcelis, L., Evers, J., 2007. Functional-structural plant modelling in crop production. In: Vos, J., L.F.M., M., de Visser, P., Struik, P., Evers, J. (Eds.), Functional-Structural Plant Modelling in Crop Production. Vol. 22 of Wageningen UR Frontis Series. Springer, Netherlands, pp. 1–12.

Walters, M. B., Reich, P. B., 1999. Low-light carbon balance and shade tolerance in the seedlings of woody plants: do winter deciduous and broad-leaved evergreen species differ? New Phytol. 144, 143–154.

Warren-Wilson, J., 1972. Control of crop processes. In: Rees, A., Cockshull, K., Hand, D., Hurd, R. (Eds.), Crop processes in controlled environment. Academic Press, New York, pp. 7–30.

Woodward, I., April 2004. Tall stories. Nature 428, 807–808.

Yan, H., Kang, M., de Reffye, P., Dingkuhn, M., 2004. A dynamic, architectural plant model simulating resource-dependent growth. Annals of Botany 93, 591–602.

Zhang, Y., Reed, D., Cattelino, P., Gale, M., Jones, E., Liechty, H., Mroz, G., 1994. A process-based growth model for young red pine. For. Ecol. Manage. 40, 21–40.

A On the implementation of LIGNUM

LIGNUM is implemented with the C++ programming language as a software library to be shared between implementations of the specific models and tree species. It is worth noting and remembering this historical background. Since its introduction (Perttunen et al., 1996, [I]), the fidelity and the most important contributions of LIGNUM to the FSTMs have been in the functional part, modelling metabolism and the allocation of metabolites. Until recently (Perttunen and Sievänen, 2005, [V]), the description of the architectural development of a tree was an ad hoc, species-specific implementation of heuristic rules embedded in the final simulation programme modelling the development of a tree crown.

The initial design principle was object oriented (Salminen et al., 1994). It appeared to be well suited for the implementation of a generic simulation tool for different tree species. In object-oriented design and programming the system is represented as a number of objects. The system development consists of defining necessary objects, their structure, functions and interconnections, and then implementing them in a programming language as reusable and extendable classes (Bossel, 1996).

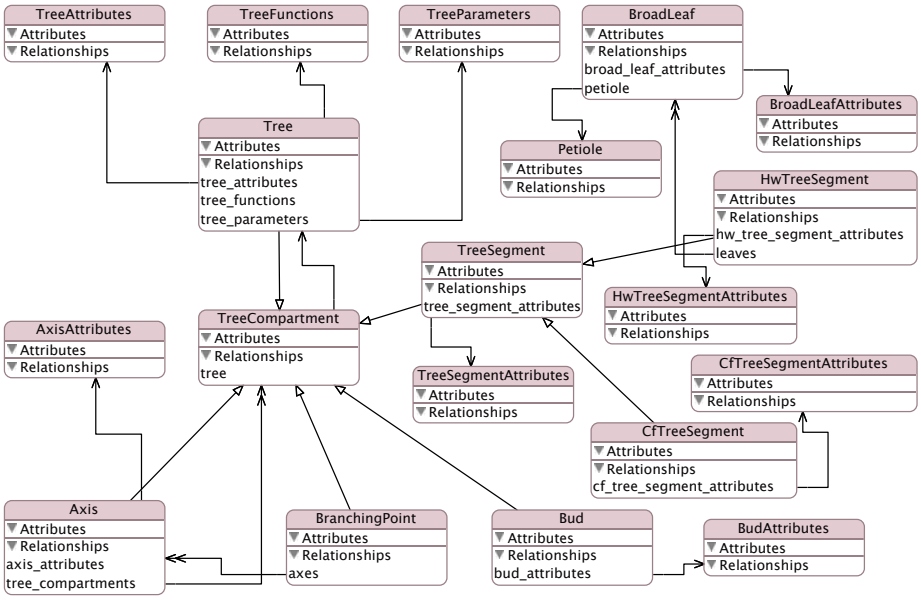


Figure 10: Data model for the most important classes in the implementation of LIGNUM. A line with single arrowhead denotes a to-one relationship between two entities, a double arrowhead line denotes a to-many relationship and an open arrowhead line denotes inheritance.

A graphical representation of the data model for the ubiquitous tree compartments and their relationships associated with any implementation with LIGNUM is given in Fig. 10. Each entity in the model is a tree compartment described in Section 3.1 and implemented as a C++ class. The information

that each class carries is geometrical and physiological. For example, the dimensions, position and orientation of each tree compartment must be known at all times, for the architectural development it is important to know whether a bud is alive, dormant or dead, for the metabolism we need to know foliage mass, intercepted radiation of each tree segment and a tree itself will keep the record of parameters and functions (e.g. photosynthetic efficiency of the foliage, metabolic and senescence rates) necessary to model tree growth.

The first implementations with Scots pine (Perttunen et al., 1996, [I]) and Jack pine (Lo et al., 2001) were encouraging regarding the programme design, but with sugar maple (Perttunen et al., 2001, [IV]) it became apparent that, beyond reparameterization of the model, using the strict object-oriented approach with concrete data types (i.e. classes), the implementation of a new tree species would be tedious, awkward and require too much recurring programming for each case.

The solution to the problem was first to identify the four ubiquitous generic algorithms to traverse the tree in LIGNUM and then implement them to operate on the topological structure in Section 3.2. We call them ForEach, Accumulate, AccumulateDown and PropagateUp[7]. Secondly, instead of implementing the entities in Fig. 10 as concrete data types these are now abstract data types. This clear distinction between algorithms and the entities they operate on is called generic programming (Stroustrup, 1997).

In practice, the implementation of LIGNUM defines the tree as a template class (using C++ notation):

```
template <class TS, class B>
class Tree{
    /*the implementation of the topological
       structure of the tree
    */
};
```

The above TS and B represent the type parameters, i.e. tree segment and bud, to be provided by the modeller. This technique defines the tree as a class that can contain different datatypes as long as constraints like subclassing and signatures are retained. The tree segment must be a subclass of either a coniferous segment or a heartwood segment and the bud must be a subclass of bud (Fig. 10).

The implementation details of the topological structure of the tree are hidden from the user of the class. Instead, to implement the functioning of the tree, the modeller defines 1) the tree segment and the bud, and 2) function objects or functors for the generic algorithms. For example, the algorithm ForEach applies a function object to each tree compartment in the tree (c.f. for_each in STL library). Typically in LIGNUM the photosynthesis (P) of a tree segment is calculated on the basis of absorbed radiation (Qabs) and the proportion of the bound solar radiation used in photosynthesis (pr). A functor that implements the photosynthesis can be defined as follows:

[7]Clearly, the design and implementation was strongly influenced by the STL library, part of C++ standard.

```
template <class TS, class B>
Photosynthesis{
    TS* operator()(TreeCompartment<TS,B>* tc)const
     {
       //check if a tree segment
       if (TS* ts = dynamic_cast<TS*>(tc)){
         double pr = GetValue(GetTree(*ts),LGPpr);
         double qabs = GetValue(*ts,LGAQabs);
         //calculate the photosynthesis
         SetValue(*ts,LGAP,pr*qabs);
       }
       return ts;
    }
 };
```

If the modeller has defined `ScotspineSegment` and `ScotspineBud` the photosynthesis of the Scots pine tree model is simply:

```
Tree<ScotspineSegment,ScotspineBud> scotspine;
ForEach(scotspine,Photosynthesis<ScotspineSegment,ScotspineBud>());
```

The modeler does not need to have any knowledge of the implementation details of the LIGNUM model, but the signature:

```
TS* operator()(TreeCompartment<TS,B>* tc)const
```

for the functors to be used with ForEach must be retained. Similarly, Accumulate is used to collect information (say, total amount of photosynthates) from the tree, AccumulateDown does the same, but in order from the tip of the branches to the base of the tree (c.f. diameter growth), and PropagateUp transfers information from the base of the trunk to the tips of the branches.

As Kurth (2000) points out, models like LIGNUM, AMAPsim and INCA, although being able to simulate different species in different conditions, have undergone historical development. Typically several developers have left their marks in the software. The reconstruction of the models implemented with these tools, for example with formal grammars, is often nontrivial and requires many times unpleasant 'sofware archaeology'. The implementation of LIGNUM with generic programming not only has made the implementation of different tree species easier, but hopefully increased the model transparency (Dzierzon, 2003).

B L system for crown architecture similar to Scots pine

The L system in Table 1 produces a crown architecture resembling young Scots pine using the L language. The symbols F, B, SB and EB describe the birth of new tree parts, and the symbols Turn, Pitch, Roll and Bend the architectural development. The parameters alpha, beta, gamma and rho are the values for branch angles. Parameters P1, P2, P3 and P4 describe the shortening of tree segments in side branches.

```
Start:          //The axiom
{
   produce F(0.30)SB()EB()B(1,1.0);
}
B(g,l):        //Bud produces tree segments and lateral buds
{
   if (g==1) //The main axis
   produce F(l)SB()Pitch(beta)B(g+1,l*P1)EB()
               SB()Roll(alpha/2.0) Pitch(beta) B(g+1,l*P1)EB()
               SB()Roll(alpha) Pitch(beta)  B(g+1,l*P1)EB()
               SB()Roll(3.0*alpha/2.0) Pitch(beta)B(g+1,l*P1)EB()
               B(g,l*P2);
  else if (g==2) //Second order branches
  produce  Bend(gamma)F(l) SB()Turn(beta)B(g+1,l*P3)EB()
                  SB()Turn(-beta)B(g+1,l*P3) EB()
                  Bend(-rho)B(g,l*P1);
  else if (g==3) //Third order branches
  produce F(l)SB()Turn(beta)B(g+1,l*P4)EB()
                SB()Turn(-beta)B(g+1,l*P4)EB()
                B(g,l*P3);
  //Fourth order branches do not bifurcate but continue to grow
  else
  produce F(l)SB()EB()B(g,l);
}
Bend(s): //Gradual bending of branches
{
   produce Pitch(s);
}
```

Table 1: L system for a pine-like structure

With parameter values alpha = 180°, beta = 45°, gamma = 17.1°, rho = 11.4°, P1 = 0.6, P2 = 0.9, P3 = 0.6 and P4 = 0.3 the crown architecture in Box 6.1, Fig. 5(a) after eight iterations is produced.

Systems Analysis Laboratory
Research Reports, Series A

A101 October 2008	Portfolio decision analysis for robust project selection and resource allocation Juuso Liesiö
A100 May 2008	Innovation incentives and the design of value networks Toni Jarimo
A99 November 2007	Modeling and on-line solution of air combat optimization problems and games Janne Karelahti
A98 January 2007	Applications of decision analysis in the assessment of energy technologies for buildings Kari Alanne
A97 November 2006	Interactive multi-criteria decision support – new tools and processes for practical applications Jyri Mustajoki
A96 May 2006	Escaping path dependence – Essays on foresight and environmental management Totti Könnölä
A95 March 2006	Advanced mobile network monitoring and automated optimization methods Albert Höglund
A94 February 2006	Affine equations as dynamic variables to obtain economic equilibria Mitri Kitti
A93 September 2005	Decision modelling tools for utilities in the deregulated energy market Simo Makkonen
A92 June 2005	Portfolio optimization models for project valuation Janne Gustafsson
A91 May 2005	Electricity derivative markets: Investment valuation, production planning and hedging Erkka Näsäkkälä
A90 March 2005	Optimal pilot decisions and flight trajectories in air combat Kai Virtanen
A89 November 2004	On foresight processes and performance of innovation networks Jukka-Pekka Salmenkaita

Systems Analysis Laboratory
Research Reports, Series B

B26 June 2006	Systeemiäly 2006 Raimo P. Hämäläinen ja Esa Saarinen, toim.
B25 May 2005	Systeemiäly 2005 Raimo P. Hämäläinen ja Esa Saarinen, toim.
B24 June 2004	Systeemiäly - Näkökulmia vuorovaikutukseen ja kokonaisuuksien hallintaan Raimo P. Hämäläinen ja Esa Saarinen, toim.

Systems Analysis Laboratory
Research Reports, Series E
Electronic Reports: www.e-reports.sal.hut.fi

E23 September 2008	Scenario-based portfolio selection of investment projects with incomplete probability and utility information Juuso Liesiö and Ahti Salo
E22 May 2008	Multi-criteria partner selection in virtual organizations with transportation costs and other network interdependencies Toni Jarimo and Ahti Salo
E21 May 2008	Markets for standardized technologies: Patent licensing with principle of proportionality Henri Hytönen, Toni Jarimo, Ahti Salo and Erkki Yli-Juuti
E20 August 2006	Smart-Swaps - Decision support for the PrOACT process with the even swaps method Jyri Mustajoki and Raimo P. Hämäläinen
E19 May 2006	Diversity in foresight: Insights from the fostering of innovation ideas Totti Könnölä, Ville Brummer and Ahti Salo
E18 June 2005	Valuing risky projects with Contingent Portfolio Programming Janne Gustafsson and Ahti Salo
E17 June 2005	Project valuation under ambiguity Janne Gustafsson and Ahti Salo
E16 June 2005	Project valuation in mixed asset portfolio selection Janne Gustafsson, Bert De Reyck, Zeger Degraeve and Ahti Salo

The reports are downloadable at www.sal.hut.fi/Publications/

Orders for paper copies:
Helsinki University of Technology
Systems Analysis Laboratory
P.O. Box 1100, FIN-02015 HUT, Finland
systems.analysis@hut.fi